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# Generic revision of the subtribe Gyrophaenina (Coleoptera: Staphylinidae: Aleocharinae) with a review of described subgenera and major features of evolution

by

J.S. Ashe

A THESIS

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1

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Date Jan 24, 1982

# Abstract

The world genera of the subtribe Gyrophaenina are revised and described subgenera are reviewed.

Comparative morphological studies of adults reveal a great variety of characters available for taxonomic and phylogenetic study when gyrophaenines are examined in sufficient detail. Structures in the mouthparts, particularly the maxilla, proved especially useful. Illustrations of variation in structural features are provided.

Gyrophaenines are inhabitants of polypore and gilled mushrooms, where both larvae and adults feed by scraping maturing spores, basidia, cystidea and hyphae from the hymenium surface. Known features of natural history of gyrophaenines are reviewed. Many of these features are related to unusual characteristics of mushrooms as habitats.

The subtribe is redefined, characterized, and larval characteristics are reviewed. The Gyrophaenina are shown to be monophyletic based on structure of the maxilla and spermatheca. Thirteen genera (11 previously described and two newly described) are recognized in the subtribe: *Gyrophaena* Mann., *Phanerota* Casey, *Eumicrota* Casey, *Encephalus* Kirby, *Probrachida* n. gen. (type species *Brachida modesta* Sharp), *Brachida* Muls. and Rey, *Agaricochara* Kr., *Sternotropa* Cam., *Pseudoligota* Cam., *Neobrachida* Cam., *Adelarthra* Cam., *Brachycara* Cam., and *Agaricomorpha* n. gen. (type species *Gyrophaena*

(*Agaricochara*) *apachaena* Seevers).

Given for each genus are, as appropriate, synonymic list, diagnosis, description, discussion of nomenclatorial and taxonomic history, notes on natural history, general geographic distribution, and review of major literature.

Based on analysis of transformation series of 47 characters, a cladistic analysis of the genera is provided. The Gyrophaenina is hypothesized to be sister group to the subtribe Bolitocharina. Within the Gyrophaenina, three lineages can be recognized, arbitrarily and informally designated the "Brachida", "Sternotropa" and "Gyrophaena" lineages. The "Brachida" lineage (*Probrachida*, *Brachida*) is hypothesized to be sister group to all other gyrophaenines, and the "Sternotropa" lineage (*Sternotropa*, *Pseudoligota*, *Adelarthra*, *Agaricomorpha*, *Brachycara*, *Neobrachida*, and probably *Agaricochara*) and the "Gyrophaena" lineage (*Eumicrota*, *Gyrophaena*, *Phanerota*) are hypothesized to be sister groups. Cladistic relationships of *Encephalus* cannot be determined at present.

Analysis of distribution of gyrophaenines among major types of host mushrooms compared with structural features in mouthparts and overlaid on a cladistic analysis of genera and analysis of major patterns of host relationships suggest hypotheses about major features of evolution of gyrophaenines.

At least two factors have had fundamental influence on evolution of relationships between gyrophaenines and mushrooms. First, evolution of mouthpart structures that allowed beetles to graze on the hymenium, rather than feed on fungal flesh, opened a relatively unused portion of the mushroom habitat. Second, general characteristics of the mushroom as a habitat require that members of each species evolutionarily optimize among conflicting requirements. These include: need to use every mushroom encountered, physiological limitations suggested by the great chemical and physical diversity of mushrooms, and physiological and competitive advantages expected from specialization. In resolving these conflicting requirements, gyrophaenines have evolved tolerance to a range of physical and chemical characteristics provided by mushrooms. This tolerance is reflected in an "acceptability spectrum" and allows members of a gyrophaenine species to respond to seasonal, yearly and geographic variation in the mushroom flora.

Major habitat types found among mushrooms, from ephemeral gilled mushrooms to persistent polypores, can be considered to provide a series of adaptive zones for gyrophaenines. Increasing reliance on hymenium scraping as a feeding mode is reflected in changes in strucuture of the maxilla. Life cycle adaptations to the ephemeral nature of gilled mushrooms was probably involved in attainment of this adaptive zone. This has occurred only among members of *Gyrophaena* and *Phanerota*. Other gyrophaenines appear to be restricted to polypores or habits are not known.

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# 1. Introduction

## 1.1 General Introduction to the Gyrophaenina

The Gyrophaenina are a subtribe of beetles in the huge, very incompletely known staphylinid subfamily Aleocharinae. As recognized in this revision, the subtribe is composed of 13 genera, within which have been described more than 500 species. This appears to be only a small portion of the extant species. More than 100 species occur in the relatively well known fauna of America north of Mexico alone, and about 20% of these are undescribed. Gyrophaenine faunas of tropical areas are inadequately known, and experience indicates that the group is very diverse there. Most described species have been placed in the heterogeneous genus *Gyrophaena* Mannerheim.

Most gyrophaenines are rather parallel-sided and more or less dorso-ventrally depressed. However, body forms are varied, including markedly robust (members of *Encephalus* Kraatz) and sub-limuloid forms (members of *Brachycara* Sharp). Generally, gyrophaenines are small to very small beetles. Size of adults is from over 3.0 mm to only 0.6 mm in length. Most are between 1.2 and 2.3 mm long.

Members of Gyrophaenina are obligate inhabitants of fresh mushrooms as larvae and adults. They live on both polypore and gilled mushrooms. Adults appear on mushrooms soon after the gills are exposed or the hymenium area becomes active, and both larvae and adults occupy more mature mushrooms. Gyrophaenines inhabit only fresh mushrooms and are usually among the first insects to appear on them.

A wide variety of staphylinids live on mushrooms. Most, however, are probably predaceous on other organisms which occur there, or, at most, are facultatively mycophagous. Gyrophaenines are unusual among staphylinids in that they are exclusively mycophagous as both larvae and adults. Additionally, gyrophaenines are unusual among mycophagous insects in that they are adapted to feed on the active spore-producing layer of mushrooms, in contrast to the more usual habit of burrowing into the flesh.

Gyrophaenines can be both abundant and locally diverse. I have collected more than 700 adults representing 13 species from a single fruiting body of *Amanita verna* (Lam. ex Fr.). While such large numbers of individuals per mushroom are exceptional, it is not unusual to collect tens of individuals per fruiting body. Hundreds of gyrophaenines can usually be collected on a brief collecting excursion whenever mushrooms are common. In addition, local diversity may be very high. Within a single small woodlot in the Blue Ridge Mountains of North Carolina, I have collected 35 species in a single season.

The subtribe Gyrophaenina has not been clearly delimited or described in detail. For this reason, the genera which have been assigned to the subtribe comprise a very heterogenous assemblage. Genera have not been adequately described and illustrations of structural features have usually not been provided. All of this has resulted in confusion about generic limits and assignments.

When I became interested in host relationships of gyrophaenines in collaboration with J.F. Cornell, it soon became apparent that little understanding of evolution of host relationships could be developed until the systematics of the group was more clearly understood. Therefore, when opportunity arose, this study was initiated.

### 1.2 Objectives of this Study

In this study, I treat in detail the systematics and evolution of the genera of the subtribe Gyrophaenina and review the described subgenera. I demonstrate that the Gyrophaenina form a monophyletic group and assign appropriate genera to it. I describe in detail and provide keys for identification of all genera. I provide a detailed discussion of known character systems and provide analysis of polarity of transformation series. Using this information, I develop initial hypotheses about cladistic relationships among gyrophaenine genera. Finally, by superimposing known natural history information, in particular host relationships, on cladistic analysis, I make first hypotheses about major features in evolution of gyrophaenines and how characteristics of mushrooms as habitats have affected patterns and processes of evolution of gyrophaenines.

This revision is intended to provide a base and stimulus for further research on gyrophaenines. I suspect many of the systematic and evolutionary conclusions reached here will require modification after the group becomes better known.

This revision is not primarily a study of host relationships and natural history of gyrophaenines. However, an understanding of gyrophaenine evolution requires consideration of natural history and host relationships. Within the limitations of this study, the treatment of host relationships cannot be exhaustive. General features of host relationships are discussed and initial hypotheses about origin and nature of host relationships are developed. I hope this discussion will stimulate more detailed studies of host relationships and evolution of this particularly interesting group of beetles.

## 2. Materials and Methods

### 2.1 Materials

This revision is based on examination of more than 15,000 adult specimens of more than 350 described and many undescribed species. Specimens representing all genera, and type material of type species of most genera included in this treatment were examined. In addition, for comparative information, specimens of both closely and more distantly related aleocharines were examined in detail.

I have collected gyrophaenines thoughout America north of Mexico, particularly in the Southeast, Southwest and Gulf States, and in Mexico and much of Canada. I have examined type material, and specimens of described and undescribed gyrophaenines from all geographic regions during visits to the British Museum (Natural History), Canadian National Collection, Field Museum of Natural History, and United States National Museum. I have received on loan type and non-type material from the British Museum, Field Museum of Natural History, Museum of Comparative Zoology, and the personal collections of J.F. Cornell and J.H. Frank. Of particular note is a very excellent collection of Mexican and Central American gyrophaenines loaned to me by A.E. Newton of the Museum of Comparative Zoology. I have received gifts of Central and South American gyrophaenines from H. Frania and South American gyrophaenines from Ian Moore.

## 2.2 Methods

### 2.2.1 Collection and Preservation of Specimens

#### 2.2.1.1 Collection

The most convenient method of collecting gyrophaenines from mushrooms is simply to remove a mushroom from the substrate and shake it sharply over a white enameled pan. Adult gyrophaenines will fall from the mushroom and may be aspirated and transferred to preserving medium. Many larvae cling to the mushroom and must be searched for between the gills or on the pore surface or in cracks and crevasses of polypore mushrooms. Larvae may also be removed from the fruiting body by dropping the entire mushroom into 70% alcohol. Larvae will quickly leave the mushroom. Because of the large quantity of alcohol required, the method is seldom practical except for very small fruiting bodies.

Many adults and larvae of species which occur on polypores, particularly resupinate polypores on logs, take refuge in cracks and crevasses at the base of the fruiting body or under flakes of bark near the mushroom. These areas should be examined for gyrophaenines.

Occasionally, gyrophaenines may be collected from leaf litter or under logs, especially at times when mushrooms are uncommon. However, this is not a reliable way to collect gyrophaenines, although members of some species (e.g.,*Encephalus* spp., *Probrachida* spp. and *Brachida* spp.)

are apparently most commonly collected in moldy litter.

Gyrophaenines are diurnal and therefore only a few adults are found in light trap samples.

It is wise to collect large series of gyrophaenines - in particular, all the individuals found on a mushroom or group of mushrooms - even if all individuals appear or are expected to represent the same species. Many samples yield a few specimens of rare or uncommonly collected species mixed with a large number of a more common species. Also, in many samples, a number of species are represented among the specimens from a single mushroom, although members of one species predominate.

There are two reasons for keeping specimens collected from each species of mushroom separate. First, in practical terms, this greatly facilitates sorting. Because of the host affinities of gyrophaenines, the number of similar species which must be distinguished within such a mixed series is greatly reduced in comparison to a mixed series from all available mushrooms in an area. A mixture of gyrophaenines from all mushrooms encountered on a collecting trip may contain 20 or more species, many represented by a large number of individuals, and many of them very similar in external structure. Sorting such a mixture can be very arduous. In particular, association of females with males is very uncertain in many samples. Second, only material in which individuals from each species of mushroom are kept separate can supply data about host associations.

Study of host relationships of gyrophaenines is of particular interest, and host information should always be collected. Specimens with host identified to species are most valuable. Although confident identification of most mushrooms is very difficult for the non-specialist, this should not deter a collector from recording whatever information can be obtained under the circumstances. Host identification to genus can be very useful. Even such information as "ex brown-spored gilled mushroom", "*ex* fleshy polypore", or "*ex* gilled mushroom on log" is useful at some levels of analysis.

In studies of host relationships of gyrophaenines, all specimens encountered on a particular mushroom or group of mushrooms of the same species should be collected. Not only may a number of species be encountered on a particular mushroom, but relative number of individuals of each gyrophaenine species is also of prime importance.

It is desirable to make a voucher collection of mushrooms from which gyrophaenines are collected. Such a voucher collection is almost essential for serious and detailed studies of host relationships of gyrophaenines. Methods and equipment required for collecting mushrooms are described in a number of popular and semi-popular books about mushrooms (e.g.,Smith and Smith 1973; Krieger 1967).

Collection of information to answer more detailed and specific questions about host relationships requires more meticulous and complex methods of sampling and handling of material and host information.

#### 2.2.1.2 Killing and Preservation

Gyrophaenines are best killed and preserved in 70% ethanol with a few drops of acetic acid added to each vial. The problem of hardening of specimens killed in alcohol is somewhat alleviated by the acetic acid.

Despite the inconvenience of hardened specimens, collection and storage in fluid has a number of advantages. Sorting of mixed collections of these small beetles is greatly facilitated. Manipulation of specimens to view diagnostic characters and direct comparison of similar specimens is much easier in fluid than with dried specimens. The optical properties of fluid make it much easier to distinguish subtle differences in punctation, sculpture and proportion which are obscured by reflections, distortion or setation in dried specimens. Many gyrophaenines have quite thin integuments which are subject to distortion upon drying. Proportions and diagnostic characters of many dried specimens are obscured or altered, making identification of a mixed series difficult. Storage in fluid allows one to conveniently keep and maintain long series of gyrophaenines. If a traditional collection of dried specimens is desired, a few specimens of each series may be mounted on points or cards.

Gyrophaenines are small, rather delicate-bodied insects, and collection into typical sawdust tubes with ethyl acetate results in many distorted or damaged specimens, especially if they are not removed promptly. Damage can be eliminated to some extent by using filter paper rather than sawdust as an absorbent medium.

A long series of gyrophaenines should not be stored dry in gelatin capsules as is done by some workers. Damage to specimens under these conditions is virtually assured even if they are packed carefully.

### 2.2.2 Dissection Techniques

Confident identification of gyrophaenines requires examination of male genital capsules. This requires digestion or maceration of the muscles around the genital capsule and subsequent dissection of the beetle for removal of this capsule.

Dried material should first be softened by washing in warm distilled water, then transferred to cold 10% potassium hydroxide (KOH) for clearing. Fluid preserved material should be handled similarly after being first rinsed in distilled water. After an entire beetle has been cleared in 10% KOH for 1 to 3 hours, depending on size, it should be washed several times in distilled water then transferred to distilled water for dissection.

It is most convenient to remove the aedeagus from inside the abdomen. This is easily done by inserting a fine needle into the membrane between abdominal segments 6 and 7. Teasing of this membrane allows separation of abdominal segments 7 to 10 with the enclosed genital capsule from the remainder of the abdomen. The genital capsule can now be removed through the proximal end of abdominal segment 7 with the aid of a very fine needle with a small hook at the tip and a pair of fine forceps.

One or both parameres should be removed from the genital capsule to provide a clear view of the lateral aspect of the median lobe.

With fresh material or material which is suitably soft, it is possible to dissect the genital capsule without clearing the entire beetle in KOH. Under these circumstances, identification is greatly speeded and one avoids the danger of clearing and subsequent distortion of a valuable specimen. However, because of strong muscles between the abdominal segments and muscles associated with the genitalia, damage to the beetle and aedeagus is more likely under these conditions. Therefore, dissection of uncleared material should be avoided except under special circumstances.

An alternative procedure is to remove the apical abdominal segments from specimens softened in distilled water as described above, and transfer these with the included genital capsule to KOH for clearing. Again, however, attempting to remove abdominal segments from uncleared material commonly results in considerable damage to the abdomen. This should be avoided if possible. As pointed out by Seevers (1951), it is a good practice to habitually place one or several males from each series into KOH for clearing.

Because most aleocharines are small, detailed study of character systems requires specialized handling. A multitude of character systems is available for analysis when these small beetles are examined in adequate detail (see Section 3.1.1).

The procedure I use for preparation of a specimen for detailed examination is the following. 1) Wash and sonicate the specimen thoroughly in distilled water to which a few drops of a mild liquid detergent have been added. Remove the soapy residue by washing in distilled water. 2) Clear the specimen 3 to 5 hours in cold concentrated KOH. Cold KOH, while slower, seems to cause less deformation than hot KOH. 3) Wash in several changes of distilled water to which a few drops of acetic acid have been added. Subsequent handling of the specimen is determined by the examination method anticipated. If one is planning to make permanent slide mounts for study, the specimen may now be transferred to 70% ethanol for dissection. 4) For reasons stated below, I prefer to examine specimens in glycerine. Transfer to glycerine must be made with care to avoid distortion or the specimen. I prefer to transfer the specimen to a mixture of 4% glycerine in 10% ethanol-distilled water. For very delicate specimens it is helpful to first make small pinpricks in the membrane behind the head, at the base of the metathorax, and near the tip of the abdomen.

The specimen should be transferred to the 4% glycerine solution in a wide-mouthed container such as a watch glass. The glycerine is concentrated by allowing water and ethanol to evaporate from the solution at room temperature, with addition of 4% glycerine as the fluid level drops. After 2 to 3 such additions the solution is allowed to evaporate as far as possible. The specimen is now ready to be transferred to concentrated glycerine on a depression slide for dissection.

Several fine minuten pins mounted on thin wooden handles plus one or more pairs of very fine pointed forceps are useful for careful dissection of these small insects.

The mouthparts should be removed for examination. This is best effected by inserting a fine needle laterally beneath the mentum through the membrane at the base of the maxillary cardo. Pressure on this point results in separation of the labium, and often one or both maxillae, from the head capsule. This exposes the bases of the mandibles and labrum for easy subsequent removal.

Abdominal segments 7 to 10 should be separated from the remainder of the abdomen as described above, and the genital capsule of males or spermatheca of females removed.

Additional dissection depends on the needs of the investigator. Removal of legs, antennae, wings and separation of the major body regions is often useful.

Because genital capsules of gyrophaenines have relatively uniform internal structure, dissections of this structure were not performed in this investigation. However, in many groups of aleocharines, internal structure of the aedeagus is very complex and study of these character systems would probably prove rewarding. Sawada (1972) offers techniques for dissection and study of internal structure of the genital capsule.

### 2.2.3 Detailed Examination

Detailed examination of the specimen plus dissected parts is conveniently done in a drop of glycerine on a depression slide at magnifications ranging from 100 to 400× (depending on working distance of the objective lens). Working with material in glycerine rather than on prepared and permanent slides has a number of advantages. Because of the complex three-dimensional structure of many of the parts examined, and the very low depth of field at high magnifications, complex structures may be difficult to interpret in light microscopy. Materials in glycerine mounts are easily oriented to view other aspects of the same structure, providing additional information about the relationships of the structural components. It also allows reorientation to observe the widest possible range of characters in the same specimen.

Dissected material in glycerine is conveniently stored in glycerine in microvials pinned through the cork and handled as regular pinned material. Structural components are easily extracted from the microvial and placed in a drop of glycerine for re-examination or observation of a newly discovered character system. Also, dissected material stored in glycerine in microvials requires no specialized storage techniques, and is less likely to be separated from the main body of a collection or misplaced, as happens with many permanent slide mounts.

I prefer to place the main body of the specimen in one microvial, and all dissected components in another, pinned beneath it. This greatly facilitates relocation of any required parts. All parts removed from gyrophaenines should be stored in transparent glass microvials rather than the semitransparent plastic microvials used by many workers. Many dissected parts of gyrophaenines are less than 0.1 mm in length, and must be located within the microvial under magnification before they can be removed for examination. Semitransparent vials preclude this and parts may be lost.

Examination of very small structures such as structure and position of sensilla requires higher magnifications (often oil immersion) than is possible with glycerine mounts, because of the very short working distances of very high magnification objectives. Material mounted on permanent slides is best for examination of these character systems.

Subsequent storage depends on the original source, degree of dissection, and future deposition of the specimen.

The body of a beetle may be mounted on a card or point and dissected parts in a microvial pinned beneath the beetle. Both beetle and dissected parts may be placed in glycerine in microvials pinned through the cork, or mounted on a permanent slide, or transferred to alcohol and stored with the remainder of the series of the same species.

Mounting a genital capsule dry in a drop of glue should be avoided. Because of the small size and thin integument of these structures, unacceptable distortion occurs on drying.

Gyrophaenines in particular and aleocharines in general are ideal subjects for examination with the scanning electron microscope. Though small, they are amazingly complex in detailed structure, especially mouthparts. Under these circumstances, the unique capabilities of the SEM are displayed to the best advantage. However, I recommend that time be taken to become thoroughly familiar with the fine structure of a beetle using light transmission microscopy before going to the SEM. This reduces the probability that SEM photomicrographs will be used to illustrate diagnostic features which are more clearly illustrated by a drawing. This also avoids confusion in orientation at magnifications possible with the SEM and allows more productive use of expensive SEM time.

### 2.2.4 Sex Determination

Males of most gyrophaenine species display secondary sexual characteristics – particularly on tergum 8 – while females of most species lack such modifications. Therefore, for most species, examination of a specimen for secondary sexual modifications is sufficient to determine its sex. However, both sexes of a few species have strikingly different secondary sexual modifications, while specimens of both sexes of other species lack external modifications.

Male gyrophaenines, and males of all other aleocharines, are recognized by presence of a tenth sternum which is lacking from females. Sternum 10 is difficult to see in many dried specimens because of telescoping of the abdomen or distortion on drying. However, presence or absence of this sternite remains the only means of distinguishing sexes by external examination of those species in which secondary sexual characteristics are lacking or similar in both sexes.

### 2.2.5 Measurements

Standardization of measurements is important for study of any group, particularly so for study of aleocharines, because body proportions are useful as both taxonomic and phylogenetic characters.

Staphylinids in general, and aleocharines in particular, offer a number of problems for accurate measurement. Thin integument and flexible body of many staphylinids result in distortion upon drying, telescoping of the abdomen, and flexure of body parts into unusual positions.

It is important that a part being measured be oriented so that it is as flat in the plane of the measuring device as possible. Also, specimens should be chosen which show as little distortion due to collecting, preservation or preparation processes as possible. Accuracy of measurement is vital. Depending on subtlety of differences measured, and size of parts in relation to accuracy of the measurement apparatus, differences can be masked or falsely implied by mismeasurement by the width of a grid or reticule line. This source of error makes it difficult to quantify, for example, small differences in relative lengths and widths of antennomeres which are distinguishable visually.

To reduce this error, the most extreme edge of a structure being measured should be oriented so that it appears just in contact with the inner edge of the measuring line. This seems to be a less ambiguous position for measurement than trying to orient the edge of the structure to the middle of the measurement line. Extrapolations between measurement lines should be made as accurately as possible.

Measurements and ratios used in this study are described and justified below.

1. Total Length (T.L.) - Total length has typically been one of the most ambiguous and difficult of major measurements of the adult staphylinid body, because of relative mobility of the body. The head, prothorax, and particularly the abdomen may be flexed into quite different planes, or segments may be telescoped into one another - a particular problem for abdominal segments of dried specimens. Various conventions for making unambiguous measurements have been suggested. In this study, I use distance from anterior margin of the labrum to apex of abdomen. The most useful range is that suggested by Herman (1972), and is taken by measuring the shortest and most contracted specimen, and the longest and most distended specimen.
2. Head Length (H.L.) - Head length is measured along the midline from the most anterior margin of the clypeus to base of head, not including the slightly sclerotized broadly triangular area at the base of the head.
3. Head Width (H.W.) - This is the greatest width at the point at which the tempora contact the posterior margin of the eye. This differs from traditional measurements

of head width in that it does not include the eyes. This measurement provides a more meaningful comparison to head length than the more inclusive measurement.

4. Head Width to Length Ratio (H.W.:H.L.) - This ratio provides a measurement of the relative transversality of the head.

5. Eye Size (E.S.) - Eye size is expressed as a ratio of total length of eye from its anterior to posterior margin compared to total head length. This ratio measures amount of lateral margin of the head which is occupied by the eyes, and is discussed more fully in Section 3.1.1.5.

   An alternative measure of eye size, not used here, is greatest width of head including eyes compared to the interocular distance. This is an indication of relative protrusion of the eyes.

6. Pronotum Width (P.W.) - Greatest width in dorsal aspect.

7. Pronotum Length (P.L.) -Length of pronotum from anterior margin to posterior margin along midline. For specimens with posterior margin of pronotum incised medially, the length is distance from anterior margin to an imaginary line tangent to the most posterior points on the posterior margin.

8. Pronotum Width to Length Ratio (P.W.:P.L.) - This ratio reflects relative transversality of the pronotum.

9. Elytra Length (E.L.) - Distance along suture from

posterior margin of scutellum to an imaginary line tangent to posterior margins of elytra. (Construction of this line is necessary because, in some specimens, the lateral angle is more posterior than the sutural angle of the elytron.)

10. Elytra Width (E.W.) – Greatest transverse distance across both elytra when in normal repose.
11. Elytra Width to Length Ratio (E.W.:E.L.) – This ratio describes the relative transversality of the elytra.
12. Elytra Length to Pronotum Length Ratio (E.L.:P.L.) – This ratio is very useful descriptively since it compares the relationship between lengths of two structures which contribute markedly to the overall habitus of the beetle.
13. Mesosternal Process to Isthmus to Metasternal Process Ratio (Ms.P.:I:Mt.P) – As discussed most recently by Seevers (1978) (see also Section 3.1.1.14), there are well defined meso- and metasternal processes extending between the mesocoxae. Length of the mesosternal process is measured from an imaginary transverse line tangent to anterior margins of mesocoxae to the most posterior apex of the process. The length of the metasternal process is measured from an imaginary transverse line tangent to the posterior margins of the mesocoxae to the most anterior apex of the process.

    In many aleocharines, these processes do not meet, and are separated by an anterior extension of the metasternum dorsal to the metasternal process, called the "isthmus". In gyrophaenines, the meso- and metasternal processes meet, and length of the isthmus is thus 0. Therefore, description of the intercoxal structures will be given as the ratio "length of mesosternal process to length of metasteral process" (Ms.P.:Mt.P.).

### 2.2.6 Illustrations

Line drawings of structural features were made with the aid of a drawing tube, with Varimag Zoom attachment, on a Wild M-20 compound microscope, at magnifications from 50 to 650 diameters depending on the structure and detail required. Scale lines are included although relative sizes of structures are not here considered taxonomically or phylogenetically important characters. Drawings were compared to the structure after inking to verify accuracy.

Scanning electron micrographs were made with two different instruments. Figures 238-244 were obtained with a Cambridge S-4 Stereoscan SEM, while Figures 233-237, 245-250 were made with a Cambridge Stereoscan 250.

Illustrations are arranged in the following order at the end of the text: 1) drawings of structural features illustrating states of taxonomically or phylogenetically important characters; 2) diagrams and figures referred to in discussions of phylogenetic analysis; and 3) diagrams and figures referred to in discussion of evolutionary trends.

Distribution maps are not provided since this revision is concerned only with superspecific taxa. Instead, distributions are given in the text.

### 2.2.7 Descriptive Format

Each description of a generic-level taxon provides reference to the original publication of the valid name of the taxon in the form in which it was first published, and the original publication of each junior synonym in its original form.

A diagnosis of each genus is given, which provides more information than the key about useful recognition characteristics. Generic determinations based on the key should be verified by reference to the diagnosis.

Following the generic description, a brief survey of the nomenclatorial and taxonomic history of the genus is provided. This is followed by a discussion of important characters for delimitation and limits of the genus. Where appropriate, a discussion of important or particularly complex structural variation is provided, along with a suggestion of character systems likely to be useful for species recognition and diagnosis, and character systems expected to be useful for phylogenetic analysis of species or species-group assemblages within the genus.

A brief review of the general natural history (e.g., habits and general host trends) of each genus is provided whenever such information is available. References to major literature discussing natural history or habits of members of each genus are given, followed by references to any descriptions or information about immature stages of members of that genus.

General distribution of members of the genus and major descriptive and revisionary literature is reviewed.

Though I have examined specimens (often type material) of about 80% of the described species of gyrophaenines, because of the large number of described species, the amount of synonymy and homonymy involved, difficulty of making accurate generic assignments based on superficial examination, and the systematic work needed within the heterogenous group of species now included in *Gyrophaena*, it is premature to attempt a detailed reassignment of species to appropriate genera. I have, therefore, included only lists of described species placed in new combination under newly described genera. Lists of described species of gyrophaenines are available in a variety of catalogues such as Fenyes (1918), Bernhauer and Scheerpeltz (1926), Scheerpeltz (1934), Blackwelder (1943), Seevers (1978), appropriate parts of Zoological Record, and major literature discussed under each generic discussion.

# 3. Systematics

## 3.1 Structure, Development, and Way of Life

### 3.1.1 Comparative Morphology

#### 3.1.1.1 Introduction

Character systems on which most taxonomic research within the Aleocharinae have been based were essentially established by Erichson (1839-49) and were later extended and more firmly entrenched by Gangelbauer (1895). Since these important studies, taxonomic research among higher taxa within the Aleocharinae has been based on number of articles of the tarsi, maxillary palpi, labial palpi and antennae of adult beetles. Many of these structures are small and difficult to see in dried specimens. Many characters previously used diagnostically at lower taxonomic levels are qualitative and difficult to describe accurately, or they vary in unexpected and undescribed ways. Also, almost all studies suffer from lack of adequate illustrations.

Few character systems generally used for systematic research within the Aleocharinae have been studied comparatively. Thus, extent of variation in character systems, and implications of that variation for taxonomic reliability and phylogenetic analysis are unknown or, at best, inadequately understood.

This lack of detailed comparative structural studies within the aleocharines, coupled with the small size of most adults and large number of valid taxa, has combined to make this the most inadequately understood large group within the Coleoptera. In fact, the complexity of the group and small size of its members have left many taxonomists with the impression that members of the Aleocharinae as a whole exhibit a basic uniformity of structure and lack character systems suitable for serious analytical study. Even Lars Brundin, after several excellent studies on athetine aleocharines, abandoned the group for study of the Chironomidae because of presumed lack and limited understanding of character systems (Brundin, 1972, p.72). Much of this erroneous opinion has resulted from use of traditional equipment and techniques. Examination of aleocharines using techniques more suited to their small size (see Section 2.2), yields a great variety of structural features for comparative morphological study at all taxonomic levels.

Although limited, the first major attempt at a general comparative description of members of the Aleocharinae was provided by Fenyes (1918) in the introduction to his monograph on the aleocharine genera of the world.

Detailed comparative structural analyses were provided by Brundin (1942, 1944, 1954 and others) for general characteristics of several athetine groups, with particularly comprehensive discussions of characters available on the male copulatory organs. Hoeg (1945) discussed variation and taxonomic usefulness of distribution of setae and bristles on the thorax of adult athetine aleocharines. However, the precedent set by the comprehensive discussions of Brundin and Hoeg has been followed by few subsequent workers.

Recently, a number of workers has begun to recognize advantages provided by more detailed study of comparative morphology within the aleocharines. Two monographs by Seevers (1957, 1965) about termitophilous and myrmecophilous staphilinids, the majority of which are aleocharines, stand out among their contemporary papers by virtue of analysis of structural variation in the included groups, and the more convincing taxonomic and phylogenetic conclusions these analyses allowed. Hammond (1975) discussed a number of seldom used character systems in classification and phylogenetic analysis of the aleocharine tribes Gymnusini and Deinopsini. Seevers (1978) provides a general discussion of systems useful for characterization of genera and tribes. Seevers concentrated on characteristics of male genitalia, and gave a far less comprehensive discussion of variation in such important character systems as mouthparts, although he recognized the importance of these structures (p.24).

Of particular importance in comparative study within the Aleocharinae are recent works by Sawada (1970, 1972). These studies, in addition to providing a comprehensive analysis of general structural variation among aleocharines, are the first attempts to provide a firm base for comparative study of the large number of useful structural characters found in the mouthparts of aleocharines. Character systems discussed in Sawada's papers have been used effectively in studies of the difficult athetine complex of genera and species by Sawada (1974, 1977) and Yosii and Sawada (1976).

In this section I introduce structural features of members of the subtribe Gyrophaenina, provide a general discussion of how these features vary within the group, and point out the extensive variety of structural features available for comparative study of gyrophaenines.

The studies mentioned above, especially those of Sawada, along with my own comparative morphological research within the aleocharines, form the basis for this discussion.

### 3.1.1.2 General Characteristics

The wide variety of basic habitus types found within the Gyrophaenina makes it difficult to give a general description of a gyrophaenine. Body builds range from very robust (specimens of *Brachycara* and *Encephalus*) to slender elongate (*Gryophaena (Phenogyra) gracilis* (Seev.)); broadly oval in outline (specimens of *Encephalus*), to parallel-sided (many species of *Gyrophaena*, *Phanerota*, *Eumicrota* and others), to sublimuloid (specimens of some *Sternotropa*, *Brachycara*, *Adelarthra* and some *Pseudoligota*); and dorso-ventrally flattened (most *Gyrophaena* and others) to broadly oval in cross section (specimens of most robust species).

The basic body outline of most specimens is reflected in proportions of the anterior part of the body. Species in which members are parallel-sided to elongate have moderately transverse to subquadrate pronota. In contrast, specimens of species which are more or less limuloid have a moderately to markedly transverse head and pronotum, associated with a relatively wide elytral base. The effect is to make them look relatively "broad-shouldered". In specimens of most of these sublimuloid species, the abdomen tapers uniformly from the base of the elytra to the apex of the abdomen.

In general vestiture, the body varies from uniformly covered with short microsetae (e.g., many species of *Sternotropa*), to microsetae moderately reduced (e.g., many species of *Gyrophaena*), to nearly bare of microsetae (e.g., *Adelarthra*). The general appearance of some species is very much affected by enlargement of some macrosetae on the thorax, elytra and/or abdomen (as in specimens of *Adelarthra barbari*). Conversely, macrosetae of some species are very small and virtually impossible to distinguish from microsetae, except in slide preparations (e.g., some *Sternotropa*, *Pseudoligota*, and *Agaricomorpha*).

The eyes are very large and prominent in members of *Phanerota*. No species of gyrophaenine have substantially reduced or absent eyes.

Antennae are very long (as long as the head, pronotum and elytra together), with antennomeres 5-10 elongate (e.g., members of the *Gyrophaena pulchella* species group) to quite short (only slightly longer than the head and pronotum together) with antennomeres 5-10 transverse (e.g., members of most species of *Eumicrota*).

Body color shows considerable variation within the gyrophaenines. Members of most species associated with polypores tend to be uniformly dark brown, piceous or black (e.g., *Agaricomorpha*, *Eumicrota*, *Sternotropa* and *Pseudoligota*). Gyrophaenines associated with gilled fungi vary considerably more in color, from uniformly dark (*Gyrophaena wisconsinica* (Seev.)), to uniformly light (*Gyrophaena compacta* Seev.). Contrasting colors are relatively common. A striking example of color contrast is exhibited by specimens of *Phanerota fasciata* Say, in which rufo-flavate ground color contrasts with black head, black outer apical third of elytra, and darkly clouded abdominal terga 6 and 7. Members of numerous other species exhibit similar, though less markedly contrasting, color patterns.

Size also differs considerably among species. Members of one to the largest species, *Gyrophaena vitrina* Casey, reach a length of 3.5 mm. In contrast, members of some undescribed species of neotropical *Eumicrota* are as small as 0.6 mm. Adults of many species of *Eumicrota*, *Pseudoligota* and *Gyrophaena* are 1.0 mm or less in length. These small gyrophaenines are among the smallest beetles known (exclusive of many ptiliid adults). Specimens of the majority of species of gyrophaenines are between 1.2 and 2.3 mm in length.

### 3.1.1.3 Microsculpture

The most common microsculpture among gyrophaenines is an isodiametric mesh with polygonal sections of cuticle delimited by sharply defined channels between the polygons. The most frequent modification of this basic pattern is a shallowing of channels so that the polygon edges are indistinctly delimited. Continuation of this trend results in complete loss of the channels between the polygons producing a smooth, strongly shining cuticular surface.

Cuticular areas exhibiting these types of microsculpture are termed "reticulate" with polygons sharply defined; "obsoletely reticulate" with polygons indistinctly defined by shallow channels; and "smooth" with polygons absent (Seevers, 1951). These states of microsculpture grade evenly into one another, and it is difficult of assign the pattern found in many beetles to one or another of these categories.

In the most generalized condition, isodiametric polygonal microsculpture is uniform over the entire body. Loss and obsolescence of microsculpture is common and has occurred numerous times independently within the gyrophaenines. Modification of microsculpture is not uniform over the body of many beetles. For example, in specimens of *Gyrophaena fuscicollis* Seev., the surface of the pronotum is obsoletely reticulate to smooth, while the surface of the rest of the body is reticulate. Microsculpture is lost from the entire body surface of some adults producing a uniformly markedly shining integument (e.g., *Gyrophaena vitrina* Casey).

The state of reticulation on various body surfaces is useful for recognition of some species. However, degree of loss of microsculpture varies among individuals. For example, microsculpture on head surfaces of specimens of *Phanerota fasciata* varies from smooth to obsoletely reticulate.

Other types of modification of the isodiametric pattern are uncommon. In members of some robust species of *Gyrophaena* (e.g., *G. arrowi* Bernh.) from South America and Africa, meshes of pronotal surfaces are markedly transverse.

Faint to marked V-shaped pairs of ridges terminating distally in a seta appear to be modifications of typical polygonal microsculpture. These types of structures are associated with the setae on tergum 10 in specimens of *Sternotropa* and *Brachycara* (Figures 171, 174) and on the abdomen of specimens of *Adelarthra barbari*.

Some types of carina found in gyrophaenines may be modifications of microsculpture. In some specimens of *Gyrophaena*, carinae associated with the setose area on the metepisternum (Figures 245, 246) follow the edge of the polygons. These carinae may result from thickening of the edges of polygons to produce a continuous ridge. In some *Gyrophaena* termination of the secondary neck carina near the gula seems to have arisen in a similar way.

Among gyrophaenines, I have not observed microsculpture modified to produce markedly scaly or pointed microsculpture as described in species of pericaline lebiine carabids by Ball (1975). Nor have I seen examples of meshes terminating in micropoints as described in gymnusine aleocharines by Hammond (1975).

Other types of integumental surfaces are found among gyrophaenines, and, though distinct from the isodiametric system of microsculpture discussed above, these modifications are small, present over a more or less substantial portion of the body, and affect the physical appearance of the integument. Therefore, these types of integumental modification ,discussed below, are considered as microsculpture.

A common integumental modification is development of small point-like elevations usually associated with setal insertions. The surface of the integument is raised into a small point with the seta inserted apically. Such small elevations are called "asperities". Numerous and closely arranged asperities, a condition termed "aperitely punctate", give the surface a rough, granular or dull, appearance. Asperities may occur in any area where setae occur, and are densest in areas where setae are most numerous. Insertions of both microsetae and macrosetae may be asperite. Asperities are found throughout the setose areas on a beetle, or are limited to one or more loosely delimited areas. They are commonly limited to, or more prominent on, the outer angles of the elytra.

Simple point-like asperities are modified in a number of ways, generally as an enlargement of the asperity to form a distinct mound, or, in more extreme examples, a spine with a seta at the end. Usually, this spine is elongated in the antero-posterior plane of the beetle. Under these circumstances the asperity is a short, low ridge or carina with the highest point most distal. These modified asperities are densely packed together as in the asperite apical angles of the elytra of *Gyrophaena sculptipennis* Casey, or widely separated and distinct as in the small carinae on tergum 7 of members of the *Gyrophaena nana* species group. Spines and carinae resulting from modifications of asperities are quite prominent in some adults. These more prominent modifications are commonly associated with secondary sexual characteristics, particularly in male specimens.

#### 3.1.1.4 Setation

Setal patterns on the body of gyrophaenines are arranged in two groups in which setae differ in prominence, permanence and characteristic types of modifications. The body of gyrophaenines is covered with a general vestiture of "microsetae". In the most generalized condition, this system consists of a uniform covering of short, densely arranged setae. Modifications of microsetae involve changes in the shape and size of setae or changes in the number and density on body surfaces, and general reduction of setae on one or more body parts. No particular setae or patches of setae in this group appear to be stable under modification.

Scattered among the microsetae are longer, darker, macrosetae with a relatively fixed position and orientation. Individual macrosetae have a permanence in location and expression not characteristic of microsetae. Modification of macrosetae is by enhancement, reduction, or loss.

Microsetae: Arrangement and orientation of microsetae, particularly on pronota and elytra, provide a number of characteristics for classification of aleocharines. These patterns have been used for classification of European aleocharines, especially athetines, since Brundin (1942, 1944 and others) and Hoeg (1944) described and emphasized the usefulness of these pattens in generic level classification. However, they have not been used for classification of the North American aleocharines previous to Seevers (1978) who described and provided illustrations of the microsetal patterns on the pronota and elytra of these beetles.

Among gyrophaenines, pronotal setae are directed caudad and more or less parallel, or are directed caudad and latero-caudad, usually radiating from a mid-apical point (Patterns A and B of Seevers, 1978). Because of lack of variability in this basic pattern, microsetal orientation and distribution have relatively little use in generic level classification of gyrophaenines.

The generalized condition among gyrophaenines appears to be a uniform body covering of short, densely arranged microsetae. Modification of the generalized condition includes changes in length and structure of setae, and/or reduction, enhancement of setae on, or loss from, one or more body regions. These modifications will be discussed more completely under discussion of the appropriate body region.

Macrosetae: Most macrosetae are longer, darker and more conspicuous than microsetae. However, in specimens of some gyrophaenines it is very difficult to distinguish between the two groups. In those instances in which macrosetae are difficult to recognize, it is often possible to distinguish them in slide preparations by differences in orientation from the more numerous microsetae.

Because of the greater constancy in location and expression of macrosetae (in comparison to microsetae), presence, absence, and degree of development of individual macrosetae are very useful characters at both inter- and intrageneric taxonomic levels. Variation in macrosetal characters is described under discussion of character systems in the appropriate body region.

### 3.1.1.5 Head

A number of character systems on the heads of gyrophaenines is available for use at various taxonomic levels. Commonly, states of these character systems form a continuum and make precise determination of character states difficult or impossible. Therefore, standardization of measurements is important. Measurements used for head dimensions in this study are described in Section 2.2.5.

Generally, a gyrophaenine head is prognathous, that is, the head is in the plane of the body with mouthparts directed anteriorly. However, in some species of *Sternotropa*, *Agaricomorpha*, *Brachycara* and *Encephalus*, head are more or less deflexed and hypognathous. Also, species of *Brachycara* and *Adelarthra* are unusual among gyrophaenines in that the base of the head is covered by the anterior margin of the pronotum

Basic shape of the head is determined by variation in at least three independently varying dimensions. These are width:length ratio, size and position of eyes, and length and shape of temporal region. The width:length ratio is a measure of relative transversality of the head. Among gyrophaenines, are species with quite transverse heads (*Adelarthra barbari*, W:L=1.7) to those with the head longer than wide (*Gyrophaena gracilis*, W:L=0.8, Figure 8). Most specimens of *Sternotropa* (Figure 17), *Agaricomorpha* (Figure 20) and *Brachycara* (Figure 19) have relatively transverse heads. In constrast, most species of *Gyrophaena*

(Figures 9-11), *Phanerota* (Figure 12) and *Eumicrota* (Figure 14) have heads which are only a little wider than long. Specimens of the *strictula* group of *Gyrophaena* (Seevers, 1951) (=subgenus *Phenogyra*) have the most quadrate heads among the gyrophaenines.

Position of eyes in gyrophaenines is generally lateral. However, in specimens of *Adelarthra barbari* , *Brachycara* species (Figure 19), and many species of *Sternotropa* and *Agaricomorpha* eyes are relatively far forward on the head and are directed more or less forward.

Eye size is difficult to estimate. Seevers (1978, p.23) compared the length of eyes to distance of an eye from base of head. This appears to be an unsatisfactory comparison because two independent variables, eye size and length of temporal region, are being compared. In this method of comparison, absolute eye size can remain the same, and relative eye size vary by change in development of the temporal region among species. Because all proportions of the head may vary independently, the comparison which most consistently reflects relative eye size (and thus overall contribution of eyes to appearance of the head) is length of eyes in relation to total head length, and is used in this study. Comparison of eye size to total head length suffers from an error factor similar to that of comparing eye length to temporal length, that is, head length may vary independently of eye size. However, head length does not vary to the extremes that development of tempora does among gyrophaenines. Also, the effect of eye size on head shape and habitus of an insect in general seems to be mostly an intuitive comparison of eye size to total head size. A more absolute comparison of eye size may be possible by comparing the eye to some unrelated structure on the same beetle, such as the scape of the antenna. However, this comparison suffers from the same deficiencies unless it can be shown that the structure being compared with eye size varies only with overall size of the beetle.

In most gyrophaenine species, eye length is about half, or slightly less than half, head length, though variability is great. The smallest eyes relative to head length are those of members of *Adelarthra barbari*, species of *Brachycara* (Figure 19), and some species of *Agaricomorpha*. The largest eyes are found in members of the genus *Phanerota*. Eyes in specimens of this genus are among the largest in relation to size of beetle known among aleocharines. Eyes of members of *Phanerota* occupy almost the entire lateral margins of the head (Figures 12, 13).

The temporal region of the head varies considerably among gyrophaenines. Specimens of most species have a relatively well developed temporal region, with the head curved broadly behind the eyes to the base of the neck. In specimens of some species (e.g., *Adelarthra barbari*, and some species of *Gyrophaena*, Figure 7), the sides of the head capsule converge from behind the eyes to the base of the head. In some species (e.g., *Gyrophaena strictula*), the head is quite quadrate with the base more or less angulate. Because of the very large size of the eyes, specimens of *Phanerota* have a very short temporal region.

Setation of the head

The dorsal surface of the head of gyrophaenines has a number of microsetae on it. These microsetae are short, stiff, numerous and densely arranged (members of *Agaricomorpha*, Figure 20; *Eumicrota*, Figure 14; and others). numerous, long and silky (*Probrachida*, *Brachida*), long and scattered (most *Gyrophaena* species, Figures 7-11), or numerous and very fine (*Brachycara* species, Figure 19). Structure and distribution of microsetae on the head of gyrophaenines seems to have undergone modification independently a number of times. Probably, presence of numerous short, stiff, closely spaced setae is the ancestral state. Reduction in number of setae and modification to produce longer or finer setae has occurred a number of times.

Macrosetae are absent from the heads of most gyrophaenines. However, there are a few notable exceptions. Heads of specimens of many species of *Brachida* (e.g., *B. exigua*, Figure 15) have a pair of macrosetae medially on the vertex. A very few species of *Gyrophaena* (e.g., *G. egena* Casey, Figure 10) have a pair of macrosetae in a similar location. It is not clear whether these macrosetae are homologous in specimens of those genera where they occur. Also, distribution of these macrosetae gives no clue about whether their presence is a derived or ancestral character state within the gyrophaenines.

In addition to this pair of medial macrosetae, many members of the subgenus *Acanthophaena* of *Phanerota* have two macrosetae on each side of the head medial to the eyes (Figure 13). Since no similar macrosetae are known among other gyrophaenines, these must be considered uniquely derived within *Acanthophaena*, probably by modification of microsetae.

### Ventral surface of head

All known gyrophaenines have an infraorbital carina (postgenal carina of Seevers, 1978). Seevers (1951) believed the large eyes of members of *Phanerota* crowded out the infraorbital carina so that members of this group lack this structure. However, he was incorrect. The large eyes of *Phanerota* species do indeed impinge on the infraorbital carinae, but they are present along the inner margin of the eye. Development of the infraorbital carinae is quite marked (e.g., many *Probrachida* species), quite weak (e.g., specimens of the *pulchella* group of *Gyrophaena*, Figure 11), or, more commonly, moderately but distinctly developed (Figures 7, 14, 20). Ventrally, the infraorbital carina extends from near the anterior margin of the eye beneath the eye, then dorsally at varying distances behind the eye, across the dorsal surface of the head as a continuous subbasal ridge or carina. In some species, the infraorbital carina is incomplete dorsally either as a result of gradual fading dorsally, or by the carina terminating near the baso-lateral angles of the head.

In addition to the infraorbital carina, all known gyrophaenines have a more posterior carina on each side of the ventral surface of the head. Depending on the species, this carina is (Figure 14) or is not (Figure 16) extended ventro-medially to contact the gular sutures. This carina also extends around the sides of the head, and in most species, terminates dorso-basally (Figure 11).

In some gyrophaenines (e.g., *Agaricomorpha apachaena* (Seev.), Figure 20) a third carina is present at the base of the head.

Other interesting characters of uncertain value on the head include relative length to width ratio at narrowest point of gula. Changes in this character seem to be related to head length. In addition, in a few gyrophaenines, the antero-lateral angles of the gula are more or less expanded to cover the base of the cardo of the maxilla (e.g., some species of *Probrachida*).

### 3.1.1.6 Antenna

Seevers (1978) pointed out the usefulness of antennal characters for classification of genera and species of aleocharines, using antennal characters extensively as important key and diagnostic characters, particularly in revision of the difficult "athetine" complex.

Actually, the number of character systems known in the antenna of aleocharines available for use at various taxonomic levels has been increasing slowly but steadily in the literature. Variation occurs principally in relative lengths and widths, and structure and setation of antennomeres, presence, absence and/or type of specialized sensilla, and overall general form. Use of antennal characters in classification of the aleocharines is presently limited by a general lack of information about variability in character systems at different taxonomic levels. As information on this variability accumulates, antennal characters are likely to become more important. In addition, more comprehensive comparative studies are likely to reveal new and presently unsuspected character systems.

Casey (1906) first used antennal characters extensively for classification of gyrophaenines. He concluded that, among the gyrophaenine genera he recognized, the antennae were variable within the generic limits of *Gyrophaena*. At supraspecific levels he recognized several important characteristics. Among most gyrophaenines, the antennomeres 1-4 are distinct from 5-11, and form a distinct pedicel for the more apical antennomeres. He also recognized that antennomere 3 is consistently longer than 4, and in most 4 is the shortest in the antenna. In addition to these general characteristics, he noted that antennomere 4 resembles either the apical antennomeres or the basal three in sculpture, setation and structure. He used this mostly in characterization of bolitocharine genera. I have not seen this character used by other authors, but it is of value at some taxonomic levels.

Based on setation, sculpture and form, the antennae of many aleocharines, especially gyrophaenines and bolitocharines, include two distinct parts: a basal portion with antennomeres weakly sculptured, with fewer, more scattered setae, and more or less conical in form, enlarged more or less gradually from base to apex; and an apical portion with antennomeres more densely sculptured, with more and denser setation, and more or less cylindrical in form, with a distinct basal angle. Among gyrophaenines the basal portion of the antenna includes either antennomeres 1-3 (Figure 27) or 1-4 (Figure 24). Most gyrophaenines have the basal portion of the antenna made up of antennomeres 1-4; only specimens of *Probrachida* have the former condition. Despite the possibility that states of this character system vary continuously among individuals of species or higher taxa, it is seldom difficult to assign an antenna found among gyrophaenines to one state or the other. (A few species of *Brachida* have antennae which show intermediate states which are somewhat difficult to interpret). Based on the distribution of states of this character in bolitocharines and other aleocharines, it seems likely that resemblance of the fourth to the apical antennomeres is the primitive condition. If this is correct, then modification of antennomere 4 to resemble the basal antennomeres has occurred independently a number of times in bolitocharines and gyrophaenines.

A number of additional patterns of antenna structure are recognizable. Generally these patterns result from variation in the relative lengths and widths of antennomeres, particularly 5-10. These patterns affect overall appearance of an antenna. Often more than one pattern may be observed in the same antenna.

Patterns of variation of relative lengths and widths of antennomeres found among gyrophaenines include:

1. Antennomeres 5-10 transverse (Figures 21, 26).
2. Antennomeres 5-10 elongate (Figure 24)
3. Antennomeres 5-10 increase gradually in width from basal to apical antennomeres (antenna appears incrassate) (Figure 21).
4. Antennomeres 5-10 uniform in width (forming a loose, parallel-sided club) (Figure 26).
5. Antennomeres 5-10 increase in relative length from base to apex (Figure 22).
6. Antennomeres 5-10 decrease in relative length from base to apex (Figure 24).
7. Antennomere 4 elongate (Figure 23), quadrate (Figure 22), or transverse (Figure 26).
8. Antenna loosely organized (Figure 23).
9. Antenna tightly organized (Figure 21).

Among gyrophaenines, these patterns are stable at a variety of taxonomic levels. Therefore, one or more of these patterns may be useful for diagnosis, characterization or analysis at several taxonomic levels, depending on the group under consideration.

Because similar types of antennal structure have almost certainly evolved a number of times within the gyrophaenines, it is impossible to use antenna structure exclusively to delimit major groups within the gyrophaenines. Seevers (1951) recognized this and rejected the subgenus *Leptarthrophaena* Scheerpeltz and Höfler of *Gyrophaena* because it was based solely on antennal characters. He also transferred the species included in the subgenus into several species groups.

However, because patterns of antennal structure vary in the same way within some groups, antennal structure frequently correlates well with other characters, such as aedeagal type or secondary sexual characteristics. Therefore, antennal structure may be very useful at a variety of taxonomic levels if considered in combination with other character systems. Patterns of antennal structure may be especially useful in recognition of species groups within such large genera as *Gyrophaena*.

In addition to the general patterns discussed above, relative lengths and widths of various antennomeres are reliable and very useful species recognition characters in many groups of gyrophaenines. Seevers (1951) used this character system extensively even though he mainly distinguished species by aedeagal characters.

I have not found any specialized sensilla on the antennae of gyrophaenines which might be useful for taxonomic purposes.

### 3.1.1.7 Labrum

Seevers (1978) stated that the labrum of aleocharines varies little and therefore has "little diagnostic value", supposedly for generic level classification. However, number and position of major setae, development, structure and relative position of major sensory elements, and presence of other characteristics such as sutures and internal setal patches vary considerably both among genera and among species. The labrum, therefore, offers a number of potentially useful character systems at various taxonomic levels.

Sawada (1970, 1972) discussed the basic structure of the aleocharine labrum and proposed terms for major setae and sensory elements.

The general outline of the labrum of aleocharines is broadly oval or trapezoidal. The surface bears a number of setae and sensory elements. Among these setae, Sawada (1970, 1972) recognized three pairs of large, suberect and darkly colored setae on each side. He distinguished three transverse rows per side, each made up of two setae. He called these rows the "distal", "medial" and "proximal" rows, and named the setae d1 and d2, m1 and m2, and p1 and p2 respectively, with the more medial seta of each row designated number 1 and the more lateral number 2 (Figure 1A).

In additon to major setae, there are a number of sensory elements (called "setulae" by Sawada) on the labrum. There is a concentration of sensory elements medially on the anterior margin. Sawada recognized three distinct pairs of sensory elements in this concentration (Figure 1A). These are: "a", a distal setiform sensillum; "b", conical and more medial; and "c", more proximal and robust, with an exposed tip.

In some taxa a pair of membranous lobes is associated with this anterior concentration of sensilla. These lobes arise on either side of the b-sensilla, and are very large (specimens of *Gyrophaena* and *Phanerota*, Figures 29, 30, 34), quite small and difficult to distinguish (*Probrachida modesta* (Sharp), Figure 37), or virtually absent (*Probrachida carinata* (Sharp), Figure 38). The base of the a-sensillum arises in these lobes in many taxa.

Sawada recognized that these setae and sensory elements were present in most aleocharines, and that their character states could be useful in classification. However, to provide a more generally useful system, especially for discussion of variation among gyrophaenines, Sawada's system of terms for setae and sensory elements must be modified and extended.

## Setae

Number of setae on the labrum varies considerably: numerous and dense (*Brachida densiventris* Cam., Figure 43; *Probrachida sparsa* (Sharp), Figure 39), reduced to only a few pairs of well developed setae (specimes of *Gyrophaena*, Figure 29; *Phanerota*, Figure 33; *Eumicrota*, Figure 35), or with a variety of intermediate states of number of setae (*Brachycara* sp., Figure 54; *Encephalus americanus*, Figure 36).

The simplest labral setation among gyrophaenines is found in specimens of *Gyrophaena*, *Eumicrota* and *Phanerota*. On the typical labrum of members of these groups distal, medial and proximal pairs are well developed and easily recognized. There is also a single seta medially on each side of the midline. For clarity, I believe a less ambiguous set of terms should be applied to these setae. Therefore, I recognize three lateral pairs of setae on each side of the labrum: an apical lateral pair, A.L.1 and A.L.2 (d1 and d2 of Sawada); a medial lateral pair, M.L.1 and M.L.2 (m1 and m2 of Sawada); a basal lateral pair, B.L.1 and B.L.2 (p1 and p2 of Sawada); and the single seta on each side of the midline, the paramedial or PM. This set of terms is illustrated in Figure 1B.

These major setae are distinguishable on the labrum of all gyrophaenines, although the homologous setae become difficult to identify in those species with a highly setose labrum. Furthermore, these setae seem to be invariant under reduction so that although the number of setae has been reduced a number of times independently within the gyrophaenines, these particular setae have not been lost or significantly reduced.

In those in which the labrum is densely setose (e.g., *Probrachida sparsa*, Figure 39), A.L.1 and A.L.2 can generally be recognized by their occurrence most near the apical and lateral margin, though quite far removed from the margin in several species of *Probrachida* (Figures 37, 38, 39). Seta M.L.2 of most specimens is recognized by its greater length in comparison to other setae, but M.L.1 on some specimens is difficult to distinguish. It is usually more proximal and slightly medial to the ε-sensillum (see below). This characteristic position is helpful in recognizing M.L.1 in species with an intermediate number of setae (e.g., *Brachycara*, Figure 54, or *Probrachida geniculata* (Sharp), Figure 40). However, this position is not invariable and helps little in distinguishing this seta in specimens of some species (e.g., *Brachida densiventris*, Figure 43; *Probrachida sparsa* (Sharp), Figure 39). Setae B.L.1 and B.L.2 are usually recognized by dark color and large size. In addition, these setae often diverge laterally, while other setae converge medially.

I have not been able to find a way to recognize which setae are homologous to PM in species with a densely setose labrum.

Other than those gyrophaenines in which the labrum is densely setose, the most common variations in labral setation are an additional seta on each side of the midline anterior to PM (e.g., *Brachida sublaevipennis*, Figure 45) and one or more setae between M.L.1 and M.L.2 (e.g., *Encephalus americanus*, Figure 36), or proximal to M.L.1 and M.L.2 (e.g., specimens of *Brachycara*, Figure 54).

It is important to note that among other aleocharines, these setae are not as stable under modification as they are among gyrophaenines. However, they serve as useful reference points for discussion of chaetotaxy of the labrum.

### Sensilla

A number of sensilla (setulae of Sawada, 1970) are on the labrum of aleocharines. Three pairs of sensilla recognized by Sawada (1970), concentrated medially on the anterior edge of the labrum, are borne by all gyrophaenines. These comprise the "antero-medial sensory area". Position, shape and relative development of these sensilla vary considerably from species to species within a genus.

The terms Sawada (1970) used to refer to these sensilla are here modified to reduce possible confusion with terms for setae. The α-sensillum (a-sensillum of Sawada, 1970) is most commonly seta-like (Figure 31). Rarely, it may also resemble a short, stubby spine (e.g., *Brachida sublaevipennis* Cam., Figure 45), or be modified to a hyaline, thickened spine (*Probrachida* undescr. sp., Figure 41). Seta-like α-sensilla are quite large (e.g., *Probrachida geniculata* (Sharp), Figure 40), more normal sized (e.g., *Gyrophaena frosti* Casey, Figure 31), or quite small (e.g., *Phanerota dissimilis* Erichson, Figure 34; *Encephalus americanus* Seev., Figure 36). Usually the base of the α-sensillum is found in the membranous lobe on each side of the midline (Figure 22), but when these lobes are poorly developed or absent, the base of the sensillum is in the main body of the labrum. Several species of *Gyrophaena* (Figure 29) have an additional small secondary sensillum at the base of the α-sensillum.

Emerging medially (between the membranous lobes when are present) is a pair of peg-like sensilla, the β-sensilla (b-sensilla of Sawada, 1970). Development of this pair varies from very prominant (e.g., *Gyrophaena antennalis* Casey, Figure 32) to quite small (e.g., *Brachida sublaevipennis*, Figure 45).

The γ-sensillum, one on each side, (c-sensillum of Sawada, 1970) is proximal and usually lateral to the β-sensillum. The γ-sensilla are usually expressed as a small internal bulbs with small conical exposed tips. Development and position relative to other elements of the antero-medial sensory area vary intergenerically and interspecifically in some taxa.

On each side of the antero-medial sensory area, on the anterior margin of the labrum, is a single seta-like sensory element, the ε-sensillum. This sensillum is present in most gyrophaenines. It is near the lateral edge of the anterior membranous lobes in most of those species in which these lobe are well developed. Development of the ϵ-sensillum among the gyrophaenines ranges from virtually indistinguishable from a seta (e.g., *Brachida sublaevipennis* Cam., Figure 45), to virtually absent (e.g., *Pseudoligota varians* Cam., Figure 51). In specimens of most species it is seta-like and more or less prominent. Development of this sensillum is quite uniform among individuals within a species, but varies among species within a genus. Ubiquity of the ϵ-sensillum makes it a useful reference point for establishing chaetotaxic homologies.

Along each lateral margin of the labrum are a number of short, spine-like sensilla arranged in a semicircular row, the "lateral sensory row". In most species there are 3 or 4 sensory elements in this row (Figure 33), but there may be as many as 5 (e.g., *Phanerota dissimilis*, Figure 34), or only 1 or 2 weakly developed spines, or the elements are virtually absent (e.g., *Encephalus* species, Figure 36, and many *Sternotropa* and *Pseudoligota* species, Figures 48, 51, 52). The sensilla of the lateral row are near or at the lateral margin (most species of *Brachida*, Figures 43-45; *Probrachida*, Figure 37-39, and *Sternotropa*, Figure 50), or more or less distant from the lateral margin (many *Gyrophaena* species, Figure 30; many *Eumicrota* species, Figure 35; and *Phanerota*). Distance of the lateral sensory row from the lateral margin seems to be more or less uniform within a genus or even at a higher taxonomic level, although secondary modifications make this character system difficult to interpret.

In addition to the character systems discussed above, internally on the labrum of some species of *Brachida* and *Probrachida* (Figure 41) is a patch of densely arranged fine hairs on each side of the midline. This patch is absent from the labrum of all other gyrophaenines.

The labrum of some species of *Brachycara* has a longitudinal suture-like clear area medially (Figure 54).

### 3.1.1.8 Mandibles

Mandibles of aleocharines are rather robust, markedly sclerotized structures. In most, the right mandible bears a more or less well developed internal tooth so that the mandibles are typically asymmetrical. Also, in some, the apex of one or both mandibles is bifid and/or part of the inner margin of the mandible is serrate. An internal membranous lobe, the prostheca, is well developed on the mandibles of aleocharines. The inner margin of the prostheca is finely ciliate or serrate.

Among gyrophaenines, the tooth on the inner face of the right mandible may be slightly (Figure 70), moderately (Figure 60), or markedly (Figure 56) developed. The medial area of the inner fringe of the prostheca is made up of bifid structures (Figures 57, 67). Though these structures are not limited to gyrophaenines, they are very characteristic of most members of the subtribe. However, some *Brachida* (Figure 65) have the medial area of the inner fringe of the prostheca with spine-like or setiform, rather than bifid, structures.

Specimens of *Brachida* have the left mandible bifid at apex (Figure 65) and specimens of a few species of *Probrachida* have both mandibles bifid at apex.

The molar region of gyrophaenines is characterized by rows of small denticles or teeth. These denticles are very numerous (*e.g.* some *Probrachida*, Figures 63, 64 ) moderately numerous (*e.g.* most *Gyrophaena*, Figure 56), or very few (some *Pseudoligota*, Figure 70). These denticles are also on mandibles of other members of the tribe Bolitocharini. Seevers (1978) suggested that these denticles may be related to fungus feeding (see Section 3.2.2.1.3).

### 3.1.1.9 Maxilla

Maxillae of aleocharines provide a rich source of character systems for taxonomic and phylogenetic study. Structure of the galea and lacinia is especially valuable. Importance of maxillary structures in systematic research has been becoming more apparent for some time, and there has been an increased emphasis placed on these characters, especially by European authors. Seevers (1978) recognized the great value of character systems in the galea and lacinia, but made almost no attempt to use character systems in these structures in his reclassification of North American aleocharines. Lohse (1974), on the other hand, pointed out that classification of aleocharines should be based principally on mouthparts, but because of the difficulty of observation, he provided a key based on other characters. Apparently, lack of comprehensive studies of character systems in the maxilla is the result of the use of traditional techniques.

Sawada (1970, 1972, and later papers) has attempted to provide a comparative base for study of these structures, describing the basic form of the maxilla of aleocharines. The terms proposed by Sawada suffer from several weaknesses. In general, it is a system for reference to the basic features of the maxilla only. He did not designate many maxillary structures which may provide systematically valuable character systems. Given the great variation in maxillary structure found among aleocharines, it would be premature to attempt to provide a more inclusive set of terms until a more comprehensive morphological base has been developed. Therefore, terms proposed by Sawada (1972) for maxillary structures have been used in this revision with only minor modifications and additions.

A generalized maxilla (Figure 2) has five parts: cardo (c.), stipes (st.) (including palpifer), maxillary palpus (mx.p.), galea (gal.) and lacinia (lac.). The cardo is an ovate, heavily sclerotized structure which articulates with the head capsule. The cardo bears a few setae, or these are reduced or absent. The stipes is divided by distinct sutures into an inner (i.sc.), medial (m.sc.) and outer (o.sc.) sclerite. These sclerites commonly bear 4 setae: 2 distally on the outer sclerite (usually the more distal of these is the longer); and a large seta near each basal corner of the medial sclerite. The inner sclerite of many aleocharines bears a number of spiniform sensilla.

The maxillary palpus of most aleocharines is composed of 4 articles. Palpomere 1 is small; palpomere 2 elongate and more or dilated distally; palpomere 3 elongate and dilated near the middle; and palpomere 4 attenuate and subulate. Members of the tribe Aleocharini and related groups have a secondary annulation of palpomere 4, so that the maxillary palpus appears to be 5-articled. Palpomere 4 bears a number of sensory elements, including a well developed spiniform apical process (a.pr.). In addition, all aleocharines have a bundle of filamentous sensilla (f.s.) basally on palpomere 4. Structure of this group of sensilla differs among species.

The outer lobe of the maxilla is the galea. Sawada recognizes two parts: an elongate proximal sclerite (p.sc.), bearing sensory pores; and a membranous distal lobe (d.l.) with some basal sensilla (b.s.) and numerous setae in most species. Shape of the distal lobe of the galea and distribution and form of setae provide important character systems for use at higher taxonomic levels within the aleocharines.

The lacinia, the inner lobe of the maxilla, varies considerably among aleocharines. Commonly, the apex of the lacinia bears a loose comb of spines with additional spines and numerous setae distributed on the inner face (see Sawada, 1972, for a discussion of variation in this structure).

Because of great variability of maxillary structure among aleocharines, the maxilla of gyrophaenines are compared, for purposes of this discussion, to the type found among members of the subtribe Bolitocharina. This comparison is useful for several reasons. First, the Bolitocharina are probably the sister group to the gyrophaenines (see discussion in Section 4.2.2.3). In addition, bolitocharines have relatively generalized maxillae which are probably more similar to those of the common ancestor of gyrophaenines and bolitocharines than maxillae of any other aleocharine group.

Maxillae of various bolitocharines are shown in Figures 96, 97 and 238. In most species of bolitocharines the four stipital setae described above are present. In specimens of a few species an additional seta is present distally on the medial sclerite of the stipes. The spinose sensilla on the inner sclerite of the stipes are well developed in most species. The maxillary palpus is generalized with numerous sensilla near the tip of palpomere 4. The two or more basal sensilla of the distal lobe of the galea are setiform, and vesiture of the distal lobe is represented by numerous, closely spaced rows of unmodified setae in most species. (But note modification of galeal setae in *Bolitochara lunulata* Payk., Figure 239).

Laciniae of most bolitocharines have a distinct comb of teeth apically (Figure 238). Teeth of this comb grade more proximally into an area of densely spaced teeth, spines and setae, proximal to which number and density of spines and teeth decrease. The entire inner face of the lacinia is densely setose in specimens of most species. Near the base of the lacinia are two or more spines separated from the spines and setae of the distal two-thirds by a more or less glabrous area.

Members of the subtribe Gyrophaenina differ from bolitocharines and are unique among other known aleocharines in that the apex of the lacinia is obliquely truncate and beset with a well differentiated patch of numerous, more or less closely spaced teeth (Figure 74). This structure, referred to as a "spore brush", appears to be adapted for scraping maturing spores, basidia and hyphae from the hymenium layer of fresh mushrooms. There is also a tendency toward reduction of teeth, spines and setae on the inner face of the lacinia. This is probably associated with reduction of function of food manipulation by the maxillae.

Co-adapted with the lacinia in relation to spore feeding are rows of setae on the outer lobe of the galea. The tendency among gyrophaenines has been to reduce the number of rows of setae and modify the setae to subspatulate or plate-like structures (Figure 235). In normal operation of the maxilla, these modified setae of the galea appear to provide a cup-like cap over the apex of the lacinial comb which probably helps retain food scraped from the mushroom surface.

The most generalized maxillae among gyrophaenines are those of specimens of *Probrachida* (Figures 81-84). Members of this genus have a well differentiated spore brush, but retain a few scattered teeth on the inner face of the lacinia. In addition, in some species, the setae on the inner face of the lacinia are numerous and not arranged in a distinct row (Figures 83, 84). Maxillae of members of this group are also generalized in that the setae on the distal lobe of the galea are unmodified and in numerous (6-10) rows. Members of *Probrachida* are unique among known gyrophaenines in the presence of teeth on the inner face of the lacinia. They share the presence of numerous rows of unmodified setae on the distal lobe of the galea with some species of *Brachida* (Figures 85-87). Numerous scattered setae on the inner face of the lacinia are also found in some members of *Brachycara* (Figure 94), and *Agaricochara* (Figure 88). Other gyrophaenines lack teeth on the inner face of the lacinia, lacinial setae in a single well-differentiated row, and four distinct rows of subspatulate or plate-like setae on the outer lobe of the galea (Figures 235, 236).

In addition to these very useful character systems, a number of other characters in the maxilla vary among gyrophaenines. Most gyrophaenines lack setae on the cardo, but members of some species of *Gyrophaena* have a single moderate to small seta on the cardo. Many gyrophaenines have a single large seta distally on the outer sclerite of the stipes, but members of *Brachycara* (Figure 94), *Agaricochara* (Figure 88), *Agaricomorpha* (Figure 95), *Sternotropa* (Figure 89) and *Pseudoligota* (Figure 92) also have a smaller more proximal seta. The one (Figure 73) or two (Figure 95) basal sensilla of the distal lobe of the galea are always setiform in gyrophaenines. In members of some species (e.g., *Probrachida*, Figure 83) these basal sensilla are difficult to distinguish from setae of the distal lobe.

Proximal to the spore brush of the lacinia of most gyrophaenines is a row of either 3 or 4 large, contiguous, inflated, clear, colorless sensilla (Figure 74). Although quite close to the proximal teeth of the spore brush or surrounded by setae, these sensillla are easily distinguished from both by their inflated, clear and colorless structure. They appear to be either modified setae or spines. Their function is unknown. Specimens of *Brachycara* and *Probrachida* appear to lack these structures.

In addition to these sensilla, there are either two (Figure 74) or three (Figure 78) more isolated, inflated, clear, colorless sensilla on the inner face of the lacinia of most gyrophaenines. Spines in specimens of some species (e.g., *Brachida*, Figure 86) in a position similar to that in which these sensilla are usually found strengthens the hypothesis that such sensilla on the lacinia are derived from modified spines.

The row of setae on the inner face of the lacinia is very long, with a large number of setae (Figures 73, 75), or shorter, with fewer setae (Figure 92). Specimens of most species of gyrophaenines have a single spine internally at the base of the lacinial face.

Number, size and density of the teeth in the spore brush at the apex of the lacinia also varies. These teeth are relatively long and widely spaced (Figures 73, 234), or far more numerous, shorter and more closely arranged (Figure 88, 236). The extreme of the latter condition seems to be reached in specimens of *Brachycara*. In members of this genus the area covered by the spore brush is very extensive, and the spore brush is made up of many hundreds of very short, very closely spaced teeth (Figure 94, 237). This variation is of particular interest because states of this character seem to correlate, in a general way, with the broad host preferences found among gyrophaenines. Specimens of groups of gyrophaenines which are most commonly found on gilled mushrooms usually have spore brushes with fewer, longer, more widely spaced teeth, while specimens of groups which prefer or are limited to woody polypores have spore brushes with more numerous, shorter and more closely spaced teeth. Members of many species which prefer hosts with have characteristics intermediate between these host types have intermediate states of the structure of the spore brush (e.g., some *Eumicrota* species, Figure 235). The reason for this correlation of structure with broad host preferences is not clear, but a relationship to feeding habits and to characteristics and availability of the hymenium layer of the host seems likely. Species with members having a spore brush of numerous, short, closely spaced teeth are included in *Pseudoligota* (Figure 92), *Sternotropa* (Figures 89-91), *Agaricomorpha* (Figure 95), *Agaricochara* (Figure 88), *Brachycara* (Figure 94), and *Eumicrota* (Figure 77). Some species of *Gyrophaena* (Figure 73), *Phanerota* (Figure 75), *Encephalus* (Figure 78), *Brachida* (Figure 85) and *Probrachida* (Figure 81) have specimens with a spore brush of large, fewer, more widely spaced teeth.

Variation also occurs in several character systems in the maxillary palpi of gyrophaenines. However, this variation seems most useful at intrageneric levels rather than intergenerically. Relative length, width and structure of the maxillary palpomeres, number and distribution of setae, and development and distribution of sensilla on palpomere 4 vary among species.

### 3.1.1.10 Labium

The generalized structure of an aleocharine labium has been discussed by Sawada (1972) and Seevers (1978). Terms proposed by Sawada for labial structures are accepted in this study (Figure 3) except that the "discal seta (d.s.)" of Sawada is here called the "medial seta (m.s.)".

Labia of members of the Aleocharinae are composed of four parts: mentum (m.t.), prementum (p.m.), a pair of glossae (gl.) and a pair of labial palpi (l.p.).

The mentum is a more or less trapezoidal sclerite which, in most aleocharines, has 3 setae near each antero-lateral angle, a pair of medial setae near the anterior margin, and one or more pairs of setae on the disc or near the postero-lateral angles (Figure 3). Characters useful at various taxonomic levels among aleocharines are degree of emargination of anterior margin, relative position and size of 3 major setae near antero-lateral margin, presence and position of additional setae, and overall shape and proportions of mentum.

The prementum includes a median (m.a.) and a pair of lateral areas (l.a.). In most, the prementum includes a pair of medial setae (m.s.), basal (b.p.), setal (s.p.), real (r.p.) and pseudopores (p.p.) (Sawada 1972). Presence of 2 medial setae in surprisingly constant among aleocharines. Gyrophaenines are unusual in that all except members of *Probrachida* (Figure 105) have a single medial seta (Figure 98) or this seta is reduced or absent (in some *Phanerota*, Figure 101).

Glossae of aleocharines are separate and relatively generalized only in the genus *Gymnusa* Gravenhorst. In other aleocharines the glossae are fused to form a "ligula" (Seevers 1978). Degree of bifurcation of the ligula has been used commonly for classification of aleocharines. Seevers (1978) believed that structure of the ligula is not as useful for classification as previously supposed, and Sawada (1972) wrote that precise degree of bifurcation of the ligula is not constant within a species. However, among gyrophaenines, I have found that general form of the ligula, whether the ligula is bifid or not, and the range of degree of bifurcation is constant within a genus or at suprageneric levels. Among gyrophaenines, at least 6 states of structure of the ligula can be recognized: 1) ligula entire, broadly rounded (members of *Encephalus*, Figure 103); 2) ligula short,entire, protruded, and broadly rounded at apex (members of *Gyrophaena*, Figure 98; *Phanerota* Figure 100; *Eumicrota*, Figure 102); 3) ligula short, protruded, parallel-sided, divided 1/2 to 2/3 distance to base into 2 more or less sharply pointed lobes (members of *Agaricochara*, Figure 110); 4) ligula short, protruded, parallel-sided, divided 3/4 to entire distance to base into 2 pointed or acutely rounded lobes (members of *Sternotropa*, Figure 111; *Pseudoligota*, Figure 113; *Agaricomorpha*, Figure 117; and *Brachycara*, Figure 116); 5) ligula short, protruded, divided to base into 2 robust, apically rounded lobes (members of *Adelarthra*, Figure 114); and 6) ligula elongate, parallel-sided, divided in anterior 1/3 into 2 divergent lobes (members of *Neobrachida*, Figure 115).

Distribution and development of sensory elements on the ligula are probably useful at a number of taxonomic levels within Aleocharinae. However, before these characters become available, extensive comparative studies will be required to determine distribution and type of sensory elements present and establish homologies between sensory elements in different groups.

The labial palpi of aleocharines are typically 3-articled. However, fusion of palpomeres, secondary annulation, or other modifications have occurred a number of times within the subfamily. In members of the tribes Aleocharini and Hoplandrini, secondary annulation of labial palpomere 3 has resulted in an additional pseudosegment. Members of the subtribe Silusina, tribe Myllaenini, and others, have the labial palpi modified to long filiform processes, and members of the Gyrophaenina (and a few others) have labial palpomeres 1 and 2 fused to produce 2-articled palpi. Degree of development and distribution of setae and sensory elements on the labial palpus provide characters useful at a number of taxonomic levels within the Aleocharinae. Sawada (1972) has provided a discussion of distribution and terms for the setae and sensory elements on the labial palpi.

### 3.1.1.11 Pronotum

Among gyrophaenines pronota vary considerably in general shape, length and width, convexity and micro- and macrosetation. Types of variation in these character systems are stable at various of taxonomic levels. Therefore, the pronotum provides a number of useful character systems, not only for characterization of taxa, but also for use in phylogenetic analysis.

## Shape

Contributing to general aspects of "shape" of the pronotum are such characteristics as width:length ratio, general shape and degree of convexity or flattening. Members of the genera *Sternotropa*, *Eumicrota* and *Agaricomorpha* have the most transverse pronota. Most members of these genera have pronota twice as wide as long or wider. In contrast, specimens of *Gyrophaena* (*Phaenogyra*) *gracilis* Seevers have quadrate pronota not more than 1.1 times as wide as long. Among members of *Gyrophaena* this character varies from very quadrate as in *G. gracilis* described above to quite transverse as in specimens of *G. hubbardi* Seevers (1.9-2.0 times as wide as long). Specimens of most species of this large genus have pronotal length:width ratios that cluster near the midpoint between these two values.

Except among members of *Gyrophaena*, pronotal length:width ratios among species within a genus do not vary greatly. Therefore, range of this ratio among species within a genus is a useful diagnostic character. In addition, length:width ratios are very useful for species discrimination, epecially in a large genus such as

*Gyrophaena*, with its great variability in this character system.

The distinctive outline of the pronotum of a gyrophaenine in dorsal aspect contributes much to the general habitus of the animal. Members of the genera *Sternotropa*, *Agaricomorpha*, *Eumicrota*, *Brachycara* and some *Gyrophaena* have basally bisinuate pronota (Figures 125, 127, 130). This character state is often associated with relatively broad pronota, and contrasts with lack of basal sinuation in many members of *Gyrophaena*, *Phanerota*, *Brachida* and some others (Figure 120, 121, 123). In members of most gyrophaenine genera, presence or absence of basal sinuation is relatively constant among species. However, within *Gyrophaena* a transformation series of this character extends from bisinuate basally to lack of basal sinuations. A bisinuate basal margin of the pronotum is widespread among aleocharines. Therefore, it is probably the primitive condition in the gyrophaenines. If so, then loss of basal bisinuations appears to have occurred a number of times in gyrophaenines. This hypothesis is discussed more fully in Section 4.1.2.

Another basic pronotal shape among gyrophaenines is broadly oval (Figure 123). Species with members with broadly oval pronota are included in *Gyrophaena*, *Brachida*, *Probrachida* and *Encephalus*. In specimens of many species of *Gyrophaena* (e.g., *G. nana* Payk., Figure 119), *Probrachida* and *Encephalus* the broadly oval outline of the pronotum is interrupted by a shallow to prominent emargination medially in the posterior margin.

The pronotum is convex or more or less flattened. Degree of convexity varies considerably among gyrophaenines. Members of species of most genera have pronota which are moderately to markedly convex. Markedly convex pronota characterize, for example, members of *Brachycara* (Figure 129), *Adelarthra* (Figure 231) and some species of *Probrachida*. Members of *Brachida*, *Sternotropa*, and others have moderately convex pronota. In contrast, members of many species of *Gyrophaena* (Figure 120) and *Phanerota* (Figure 123) have very slightly convex to almost flat pronota.

Degree of convexity of the pronotum is related to another characteristic of the prothorax. The hypomera of the prothorax are either inflexed and hidden by the lateral margins of the pronotum in lateral aspect, or are deflexed and more or less visible below the lateral margins of the pronotum. Amount of the hypomera visible varies considerably among gyrophaenines from only a small portion of the anterior margin to most of the hypomera. Variation in this character also occurs among other aleocharines. Seevers (1978) suggested that the generalized form of the aleocharine prothorax may have been convex with hypomera invisible in lateral aspect. Therefore, subsequent flattening of the prothorax, exposing the hypomera would be a derived condition. This implies that exposure of the hypomera is directly related to convexity of the prothorax. While correlation between convexity and exposure of the hypomera is striking among gyrophaenines, other factors may also be involved in exposing the hypomera. A correlation between exposure of the hypomera and relative width of the pronotum is also evident. Relative narrowing of the pronotum may result in rotation of the hypomera from a markedly inflexed to a more deflexed orientation, resulting in exposure in lateral aspect. It is impossible at this time to be certain which of the factors – degree of convexity or relative width – is more important in hypomeral exposure. Probably these two factors do not vary independently and flattening of the dorsal surface of the pronotum is normally associated with a decrease in relative width.

Among gyrophaenines, the hypomeron is broadly exposed only in members of most species of *Gyrophaena* and *Phanerota*. However, variability in this character among members of *Gyrophaena* is marked, and the range extends from hypomera not visible in lateral aspect, to fully exposed. Therefore, exposure of the hypomera is not a distinguishing characteristic of *Gyrophaena* as was suggested by Seevers (1951, 1978).

Another characteristic which contributes to overall shape of the prothorax is degree of ventral deflexion of antero-lateral margins of the pronotum. Marked deflexion of this region is evident among members of *Encephalus* and

*Probrachida modesta* (Sharp). Expression of this character differs considerably among gyrophaenines from the extreme examples of antero-lateral defelexion mentioned above, to lack of deflexion in most *Gyrophaena* and others.

Setation

Both macrosetae and microsetae are present on the pronotum. There is no clear correlation of variability in these two systems. Although most gyrophaenines with large numbers of well developed microsetae on the pronotum have weakly developed macrosetae, and *vice versa*, this relationship is not invariable.

Microsetae. – Pronota of most gyrophaenines are uniformly covered by a dense vestiture of microsetae. Generally, microsetae are directed posteriorly or postero-laterally. Pronotal setal patterns among gyrophaenines correspond to Patterns A and B of Seevers (1978), and are not very useful for discrimination of taxa. Pronotal microsetae are either very short and stiff (e.g., members of *Sternotropa*, *Agaricomorpha*), long and silky (*Brachida* species), or a variety of intermediate lengths and stiffnesses. Modification of pronotal microsetae has generally been by reduction of number and prominance of setae. This reduction appears to have occurred independently in a number of lineages. Specimens of *Adelarthra barbari* Cam. (Figure 231), *Encephalus*, *Phanerota* and many species of *Gyrophaena* have pronota virtually bare of microsetae. Variation in pronotal microsetation among species within some genera (*e.g.*, *Gyrophaena*, *Eumicrota*) encompasses a range of pronotal vestitures, from a dense covering of numerous stiff setae, to few, scattered, small setae. Generally, however, development of microsetae on the pronotum shows relatively less variation than these extremes among species within a genus.

Macrosetae. – These are in three distinct longitudinal rows on each side plus an additional anterior seta on each side of the medial row (Figure 4). For ease in discussion, setae in each row are numbered consecutively beginning with the most anterior seta. The most lateral of these rows of setae begins with the seta in the antero-lateral corner of the pronotum. There are four setae in the lateral row, labeled L1-L4. Immediately mediad of the laterals is the "mesolateral" row, with three setae (ML1-ML3). Immediately mediad of ML1 on the anterior margin is a single "paramedial" seta (PM). On each side of the midline is a row of four setae, the "medials" (M1-M4).

The generalized arrangement of setae described above is found in most species of *Gyrophaena*, *Phanerota* and *Eumicrota*. However, in many species of *Gyrophaena*, M2 is absent (*e.g.*, members of the "*keeni* group" of Seevers, 1951), and macrosetae are difficult to see in specimens of *Eumicrota*. On specimens of many species macrosetae are difficult to distinguish from microsetae, and on some can be seen only in cleared preparations by examination with a compound microscope. Difficulty of distinguishing macrosetae is often correlated with density of microsetae. Conversely, reduction in number of microsetae is commonly correlated with increased prominence of the macrosetae. This may be clearly seen in members of the genus *Eumicrota* by comparing figures of the pronotum of *E. socia* (Figure 125) and *E. corruscula* (Figure 124). These figures are somewhat misleading because the macrosetae on the pronotum of *E. socia* are much less prominent than they appear in the drawing.

Variation in macrosetae includes the following conditions. Macrosetae appear to be absent or are indistinguishable from microsetae in specimens of many species of *Pseudoligota*. ML2 is absent from some members of many genera (e.g., *Agaricomorpha*, *Brachycara*, *Sternotropa* and others). L2 is absent from members of *Brachida*, *Brachycara* and *Agaricochara*. In specimens of some species of *Sternotropa*, *Adelarthra* and *Brachycara*, L3 is more or less prominent in comparison to other pronotal setae (greatly so in *Adelanthra*).

Variation in these, and other, characteristics of development of pronotal microsetae may be useful at a number of taxonomic levels. However, before these character systems can be used confidently, a more complete understanding of both interspecific and intergeneric variation is needed.

### 3.1.1.12 Elytra

Length and width of elytra in relation to the pronotum are taxonomically important characteristics since these attributes contribute considerably to overall habitus of a beetle.

Elytra of most aleocharines are rather generalized and longer than the pronotum. However, members of some tribes have elytra which are considerably shortened (Seevers, 1978). Small size of elytra is associated with aptery or brachyptery and hence flightlessness. Neither brachypterous nor apterous gyrophaenines are known. However, among gyrophaenines length of elytra relative to pronotal length ranges from much longer than the pronotum (e.g., members of *Agaricochara* species), to about equal to pronotal length (most *Gyrophaena*, *Phanerota* and others) or slightly shorter than pronotal length (most *Brachycara*).

Lateral apical angles of the elytra are markedly sinuate (e.g., *Encephalus zealandicus* (Figure 134), moderately to slightly sinuate (e.g., *Eumicrota*, Figure 133), or not at all sinuate (e.g., most *Gyrophaena*, Figure 131; *Phanerota*, Figure 132).

Both microsetae and macrosetae are on the elytra of aleocharines. Distribution and development of these setal patterns, while difficult to quantify, may be important at a variety of taxonomic levels. Among aleocharines are fewer microsetal patterns on the elytra than on the pronotum. Seevers (1978) recognizes only three. Among gyrophaenines elytral microsetae are subparallel and directed caudally (Pattern R of Seevers, 1978). Microsetae are very numerous and densely distributed so that the elytra appear more or less markedly pubescent (e.g., specimens of *Brachida* species), or are very few and very sparsely distributed e.g., specimens of *Adelarthra barbari*). Specimens of most species of gyrophaenines have an intermediate condition (e.g., most *Gyrophaena* species). Length of microsetae also differs from long and silky (members of *Brachida*) to very short and stiff (e.g., most *Sternotropa*).

In some aleocharines distribution of microsetae on the elytra is not uniform. This condition is not common among gyrophaenines, though the elytra of specimens of some species are narrowly asetose along the suture.

Figure 132 illustrates the distribution of macrosetae on the elytra of most gyrophaenines. Development of these macrosetae is quite variable among genera and species. Macrosetae are small, inconspicuous, or obsolete (most *Pseudoligota* species), moderate sized and more or less conspicuous (most *Gyrophaena* and *Phanerota*), or extremely large and very conspicuous (members of *Adelarthra barbari*). Development of macrosetae may vary among species within a genus (e.g., species of *Sternotropa*) in which instance it becomes a useful character at the species or species group level, or development of macrosetae may be relatively constant within a genus.

Setal punctures may be asperite or not. In particular, many males have an large asperities on various parts of the elytra as part of the secondary sexual complex.

Elytra of specimens of some species of gyrophaenines are adorned with spines, carinae, low elevations or depressions. Most often these modifications of the elytra are, along with asperities, part of the secondary sexual complex of characters.

### 3.1.1.13 Prosternum

Character systems of the prosternum have been used consistently by few authors. Generally, in aleocharines, the prosternum is a more or less transverse bar between and in front of the anterior coxae. In some aleocharines (members of the tribes Falagrini and Dorylomini), the prosternum is prolonged behind the anterior coxae and contiguous with or fused to enlarged mesospiracular peritremes. The posterior prolongation of the prosternum of some aleocharines is near or adjacent to lateral extensions of the prothoracic hypomera, such that the anterior coxal cavities are more or less closed behind (Seevers, 1978).

Among gyrophaenines, the prosternum is markedly (Figure 147), moderately (Figure 145), or slightly transverse (Figure 144). In general, degree to which the prosternum is transverse correlates well with the width:length ratio of the pronotum. Thus, gyrophaenines which have a markedly transverse pronotum also have a relatively transverse prosternum. However, other factors also affect expression of this character. The prosternum of some gyrophaenines is a narrow bar with little posterior extension between the coxae, but in others extends posteriorly to various degrees between the anterior coxae as a broad process. A broad prosternal process may reduce the width:length ratio of the prosternum independently of pronotal width.

The prosternum is generally horizontal, but in specimens of a few species (e.g., *Encephalus americanus*) , the prosternum is more or less declivous posteriorly.

The prosternum of some gyrophaenines is ornamented by various carinae, spines, or knobs. Most specimens of *Gyrophaena*, *Eumicrota* and *Encephalus* have a fine transverse carina extending from the antero-lateral margins of the prosternum posteriorly and medially (Figure 142). A similar, but more marked, transverse carina on specimens of *Adelarthra barbari* protrudes medially as a prominant transverse tooth. Specimens of *Agaricomorpha*, *Sternotropa*, *Brachida* and *Pseudoligota* lack this transverse carina, but have a more or less marked medial knob, carina or spine. The prosternum lacks ornamentation in specimens of some species (*e.g.*, some *Phanerota*, Figure 144). These prosternal character states are useful at a variety of taxonomic levels. The general form of the modification (e.g., with transverse carina or with medial protuberance) is consistent among members of many higher taxa, while the specific form of the general type of modification may vary interspecifically.

In the great majority of gyrophaenines, the inner edge of the hypomera and the postero-lateral margins of the prosternum are very widely separated. However, in at least one species, *Sternotropa brevicornis* Cam., anterior coxal cavities are nearly closed behind by the approximation of these parts.

### 3.1.1.14 Mesosternum and Metasternum

The mesosternum and metasternum provide several character systems useful at a variety of taxonomic levels. Among most aleocharines, the middle coxae are contained in deep acetabula formed by these sclerites. In specimens of most species the edges of the midcoxal acetabula are margined with a fine bead (Seevers, 1978).

Mesosternum

Among gyrophaenines, the mesosternum is well developed and quite broad in front of the midcoxae. In specimens of many species of gyrophaenines, the mesosternum has a medial longitudinal carina. This carina is well developed and extends from the distal edge of the mesosternum to the apex of the process (e.g., specimens of *Agaricomorpha*, Figure 148), or it is more or less reduced, present only anteriorly on the mesosternum and absent or obsolete before the apex of the metasternal process. Specimens of some species lack the mesosternal carina, but have in the same position a more or less diffuse, low to very low ridge (e.g., *Brachycara*, Figure 250). Still other gyrophaenines lack any medial modification so that the mesosternum is smooth medially (species of *Gyrophaena*, *Phanerota* and *Eumicrota*; Figures 150, 151). In most instances, presence or absence of a medial carina or low ridge is constant among members of a species within a genus, or even at suprageneric levels.

Many other aleocharines have a similar carina, and a complete, well developed carina is characteristic of most bolitocharines. Probably presence of a medial longitudinal carina on the mesosternum is primitive within the gyrophaenines, and reduced conditions derived.

The mesosternum of most gyrophaenines is more or less horizontal, but the mesosternum of members of *Encephalus* is abruptly turned dorsally in front of the middle coxae so that it is more or less vertical in lateral view.

The mesosternum of most aleocharines has a medial posterior process more or less extended between the middle coxae. Among gyrophaenines, this process is very broad and extends a considerable distance between the midcoxae (discussed further below).

Intercoxal Process

The beaded margin which delimits the midcoxal acetabula also delimits a pair of processes, on each of the mesosternum and metasternum, which extend more or less between the midcoxae. Among aleocharines these intercoxal processes differ in length, width, distance each process extends between the coxae, and degree of separation of apices of the processes. In those instances in which the mesosternal and metasternal processes are not contiguous, they are joined by an anterior extension of the metasternum termed the "isthmus" (Seevers, 1978). The isthmus is extended anteriorly beyond the margined apex of the metasternal process and, most aleocharines, is in a more dorsal plane than the metasternal process. Relative development of the mesosternal process, isthmus and metasternal process between the middle coxae, and degree of separation of the middle coxae by these processes provide very useful character systems at generic and suprageneric levels. Measurement of relative lengths of these processes is discussed in Section 2.2.5.

In members of the subtribe Gyrophaenina, the intercoxal processes are very broad between the middle coxae, so that the coxal cavities are widely separated (Figure 149). In addition, in most gyrophaenines, the mesosternal and metasternal processes are broadly contiguous or fused between the coxae, and the isthmus is absent. In specimens of *Agaricochara laevicollis* (Figure 152), the apices of the intercoxal processes are very slightly separated and there is a short isthmus (relative lengths 7:0.5:4).

The apices of the processes at the juncture are truncate or broadly rounded. The junction between the intercoxal processes is delimited by a distinct suture

(Figure 149) (e.g., most *Gyrophaena* and *Phanerota*), or the processes are more or less indistinguishably fused (Figure 154) (e.g., most *Sternotropa*, *Brachycara*, and *Pseudoligota*). In many gyrophaenines with fused processes, the juncture between them is slightly beaded, or the processes are distinguished by differences in microsculpture. Under these conditions, relative lengths of the processes may be estimated. In other gyrophaenines, the processes are indistinguishably fused (*e.g.*, in many *Pseudoligota*) and accurate estimates of the relative lengths of the processes cannot be made.

Relative lengths of the two processes provide useful character systems at the generic level in gyrophaenines. Among members of most genera, variation in this character system is relatively slight, but is quite extensive in a few genera (e.g., *Gyrophaena*). This character system should therefore be used with caution. In most members of *Agaricochara*, *Phanerota*, *Eumicrota*, *Sternotropa* and *Brachycara*, mesosternal process attains the middle of the coxal cavities, or slightly posterior to the middle of the coxal cavities. Among members of *Gyrophaena* the mesosternal process is various from extended to slightly posterior to middle of the coxal cavities, to extended to the apex of the coxal cavities. In specimens of *Brachida*, the mesosternal process attains or almost attains the posterior margin of the coxal cavities. In specimens of *Encephalus*, the mesosternal process extends to the posterior margin of the midcoxal cavities so that the metasternal process is absent.

### 3.1.1.15 Metepisternum and Metepimeron

These two elongate pleurites are immediately dorsal to the metasternum. In the generalized condition, these sclerites are covered uniformly with numerous irregularly scattered setae. Among gyrophaenines, this condition is present in specimens of *Probrachida*, *Brachycara* and some species of *Brachida* (Figures 158, 249). All bolitocharines (=group Bolitocharae of Seevers, 1978) and many other aleocharines also have numerous irregularly scattered setae on these pleurites.

Modification of this generalized condition has occurred a number of times in the aleocharines. Modification has in most instances resulted in reduction of the number of setae on the metepimeron to a few scattered setae near the posterior margin, and reduction of the setae on the metepisternum to two irregular rows, one well developed row, or loss of setae from this sclerite altogether.

Among gyrophaenines, in addition to the generalized state described above, three states of the number and development of setae on the metepistenum are recognized. In specimens of *Pseudoligota*, many *Agaricomorpha* and many *Sternotropa*, the setae on the metepisternum are in two irregular rows (Figures 159, 160, 248). In specimens of *Adelarthra* (and *Encephalus zealandicus*) only a few scattered setae are present on the posterior third of the metepimeron.

In specimens of *Gyrophaena*, *Phanerota* and *Eumicrota* setae on the metepisternum are in a single more or less well developed row. In addition, in specimens of some species of *Gyrophaena* and *Phanerota* this single row of setae is bordered anteriorly and ventrally by a more or less indistinct carina (Figures 156, 246).

To my knowledge, this character system has not been studied previously among the aleocharines. Therefore, distribution of the states of this character, and taxonomic levels at which these characters are stable are inadequately known. The general usefulness of this character system within the aleocharines is thus uncertain. States of this character system in gyrophaenines are more or less stable at the generic or suprageneric level. However, a single well defined row of setae has apparently evolved several times within the gyrophaenines. This is indicated by presence of both numerous scattered setae and a single row of setae among members of the same genus (e.g., *Agaricomorpha*).

### 3.1.1.16 Legs

As pointed out by Seevers (1978), legs of most aleocharines do not have outstanding characters for taxonomic study. Number of tarsomeres per leg differs in different groups, and this has been used in constructing classification systems that seem artificial (see Fenyes 1918, 1921). However, while tarsal formula should not be ignored, it is not, taken alone, a reliable character system for recognition of monophyletic groups (Seevers 1978).

All gyrophaenines and most other members of the tribe Bolitocharini have a 4-4-5 tarsal formula, but this formula is not limited to this group.

Aleocharines have an empodial seta between the tarsal claws. This seta is shorter than, as long as, or longer than the tarsal claws. Among gyrophaenines, the empodial seta is shorter than the tarsal claws.

Relative lengths of tarsomeres 1 and 2 of the hind leg is characteristic of many genus-level or suprageneric-level groups among gyrophaenines. Hind tarsomere 1 of gyrophaenines has a more or less distinctly developed ventro-lateral ctenidium of 6 to 15 or more setae (Figure 161). The ctenidium is probably involved in cleaning activities.

### 3.1.1.17 Wings

All known gyrophaenine adults are fully winged. Since adults must seek and colonize emphemeral, unpredictable and more or less widely dispersed habitats, loss of wings seems unlikely. Should a flightless gyrophaenine be found, the apterous or brachypterous condition would suggest that its members have fundamental differences in natural history from other gyrophaenines.

Figures 137-140 show the variation in shape and vein patterns found among species of several genera of gyrophaenines. Figure 141 of the wing of *Venusa* sp.

(subtribe Bolitocharina) is included for comparison. There is little significant difference in the wings examined. In general, specimens of smaller species have wings slightly more obtusely rounded apically, with less extensively developed veins.

### 3.1.1.18 Abdomen

Abdominal structure of staphylinids has been described in detail by Blackwelder (1936) and that of aleocharines by Fenyes (1918) and Seevers (1978). Interpretation and numbering of segments presented by Seevers (1978) is accepted in this revision.

Abdomens of aleocharines are composed of 10 segments, the last two of which are modified in connection with the genitalia. Terga 1 to 8 each bear a pair of spiracles. Segment 1 is more closely united to the metathorax than to the remainder of the abdomen. Both segments 1 and 2 are usually covered by the elytra and are not visible in repose. Sterna of segments 1 and 2 are membranous and not distinguishable (except for a second sternum secondarily present in a few termitophilous aleocharines (Seevers 1978)). Segments 3 to 7 have, in addition to a tergite and sternite, a paratergite and parasternite on each side. Segment 7 has no parasternites and segment 8 has only a tergite and sternite. The tergum of segment 8 has secondary sexual modifications in many aleocharines, especially in the male. These provide numerous characters for use at specific and higher taxonomic levels. In all aleocharines except *Gymnusa*, the tergite of segment 9 is divided into two lateral lobes. Only the male has a ninth sternite.

Among gyrophaenines, general shape of the abdomen, punctation, setation and shape and proportion of sclerites provide taxonomically useful character systems. Additionally, one or more of terga 3 to 7 may have a more or less pronounced transverse concavity.

Also, among all gyrophaenines, the anterior margin of tergum 7 is modified for openings to abdominal glands. The distribution of this modification among other aleocharines is not known.

### 3.1.1.19 Abdominal Tergum 10

To my knowledge, character systems on abdomimal tergum 10 have not been previously used extensively in study of the aleocharines. However, tergum 10 contains a number of character systems of potential use at a number of taxonomic levels. These include: shape of the tergite, distribution of micro- and macrosetae, structure of micro- and macrosetae, and presence or absence of secondary sexual character states.

The generalized aleocharine condition of tergum 10 is a flat trapezoidal sclerite in dorsal aspect, with a more or less dense patch of microsetae occupying the middle of the dorsum of the tergum. Probably, in the most primitive condition, this patch of microsetae was large, occupying most of the dorsal surface, and was made up of numerous, densely arranged, unmodified setae. Most aleocharines also have three macrosetae (4 in some) on each side of the tergum near the posterior and postero-lateral margins. Modification of these character systems is quite extensive among aleocharines. While these may be useful for higher classifiction of aleocharines, distribution and variation in states of these systems need study throughout the aleocharines before they can be applied effectively.

Among gyrophaenines a number of character systems of tergum 10 are useful in studies of classification and relationships of higher taxa. Specimens of *Probrachida* and *Brachida* exhibit the generalized condition described above (Figure 168). Specimens of *Gyrophaena*, *Phanerota*, *Agaricochara* and some *Pseudoligota* retain a more or less square microsetal patch (setae reduced in number in some species), but with microsetae more or less flattened and subspatulate (Figures 162, 164, 169). Loss of setae antero-medially and postero-laterally results in one or a few rows of setae arranged in a distinct "V". This distribution of microsetae is found only among members of *Eumicrota*. From the generalized condition, loss of setae postero-medially results in a patch with an inverted "V"-shape (here termed "chevron-shaped"). A chevron-shaped setal patch characterizes members of *Agaricomorpha* (Figure 175) and some *Sternotropa*. Continuation of this trend towards loss of setae postero-medially and antero-laterally produces a chevron-shaped patch made up of two (faintly 3 in some) distinct rows of setae. This last condition characterizes most *Sternotropa* (Figure 170, 171), members of *Brachycara* (Figure 174) and *Neobrachida*. Microsetae on tergum 10 are flattened and subspatulate in most gyrophaenines.

Additional modifications of character systems on tergum 10 found among gyrophaenines include: elongation of the tergum posterior to the setae in some *Gyrophaena* (e.g., *G. flavicornis* Melsh. and *G. fuscicollis* species group); an additional macroseta on each side of the tergum (in males of the *Gyrophaena pulchella* species group); and secondary sexual modifications of tergum 10 in some *Gyrophaena* (particularly notable in members of the *G. coniciventris* species group (see Seevers,1951)).

Additional study of structure of tergum 10 would probably reveal other useful character systems.

### 3.1.1.20 Female genitalia

The vulva and vagina of most aleocharines are relatively simple. In some athetines, these are sclerotized and have spines, setae or hooks (Seevers 1978). Brundin (1942) has illustrated characteristics of the vagina of athetines. The vagina of gyrophaenines does not contain extensive sclerotized areas or hooks and spines. However, it would be surprising if internal structure of the vagina were not in some way modified in relation to the very complex and varied structure of the median lobe of the aedeagus. Peschke (1978) found this to be so in females of *Aleochara curtula*. However, this has not been investigated in gyrophaenines.

Spermathecae of gyrophaenines are sclerotized, the shape being characteristic of species or higher taxa in many groups. Form of gyrophaenine spermathecae is unique among aleocharines, as far as is known, in that it has a lateral plate-like flange on the neck (Figure 176). (Compare with spermatheca of *Bolitochara*, Figure 191.) The spermatheca is simple (for example, in members of *Gyrophaena*, Figure 176; *Eumicrota*, Figure 181; and *Agaricochara*, Figure 186), has the neck elongate proximal to the lateral flange (in members of *Phanerota*, Figure 179, 180), or has the neck elongate distal to the lateral flange (in members of *Brachida*, Figure 184).

### 3.1.1.21 Male genitalia

Male copulatory organs of aleocharines have been described in detail by Brundin (1942), Welch (1964), Sawada (1972), Peschke (1978) and Seevers (1978). All of these descriptions are quite detailed and differ little in interpretation of aedeagal structure. However, they differ somewhat in terms proposed for these structures. In this treatment, I will accept those proposed by Seevers (1978). A brief summary of the more detailed account in Seevers (1978) is necessary for discussion of this structure. The aedeagus of male aleocharines is unique among staphylinids.

It is made up of a more or less tubular median lobe and two mobile lateral lobes, or parameres. The aleocharine median lobe is not fundamentally different from that of other staphylinids, but the parameres are very distinctive. While parameres of other staphylinids are slender and made up of only a single sclerite, those of aleocharines are expansive and made up of at least three distinct interarticulating sclerites.

Median lobe: structure of a generalized aleocharine median lobe is shown in Figure 5A. It is a more or less tubular structure with an enlarged bulbous basal portion, and a more slender cylindrical apical part. The ejaculatory duct enters an internal sac (in.s.) which is everted into the vulva of the female during copulation. In many aleocharines, membranes of the internal sac are armed with numerous spinules, plates, and sclerotized areas which probably aid in correct placement of the sac in the vulva. A slender, more or less sclerotized, flagellum (f.) is present in the internal sac. The flagellum is hollow and functions to introduce sperm into the female tract. It is very long in many aleocharines an is probably inserted into the female spermathecal duct during copulation. On the underside of the median lobe is an oval sclerite which is attached to the main body of the median lobe by a thin membrane. This sclerite, the compressor plate (c.p) is moved by dorso-ventral muscles (dv.m.) which originate on the upper surface of the base of the median lobe.

Contraction of the dorso-ventral muscles pulls the compressor plate into the body of the median lobe, increasing the hydrostatic pressure and causing eversion of the internal sac. The internal sac is retracted by a set of longitudinal muscles (l.m.) which originate on the proximal surface of the bulbous base.

The ejaculatory duct (ej.d.) enters the median lobe through the median foramen (m.f.). In front of the median foramen are a pair of condyles (p.c.) on which the parameres articulate. Sclerotized phragmata on the base of the median lobe serve as attachment for muscles of the parameres. A distal crest (d.cr.) in front of the paramere condyles and a proximal crest (p.cr.) behind the median foramen are present in many. Other thickenings for muscle attachment are present in some.

Distally, the median lobe terminates in a more or less slender apical process (a.p.). The apical process is highly modified in many aleocharines and is very useful in systematic study at both species and higher taxonomic levels.

In many aleocharines, there is a hinged sclerite, the ostial lamella (o.l.), which closes the apical orifice of the median lobe when the internal sac is in repose.

A generalized gyrophaenine median lobe is shown in Figure 5B. The gyrophaenine median lobe differs primarily in that there is no eversible internal sac. Instead, a more or less tubular or cylindrical flagellum is exerted and slides in and out of the basal portion of the median lobe in response to hydrostatic pressure or contraction of longitudinal muscles. It is not certain that this flagellum is homologous to that found in the internal sac of other aleocharines. The median lobe does not have a complex internal array of spines, plates, or sclerotized areas.

At the base of the flagellum of gyrophaenines is a more or less membranous, transparent, globular structure, the function of which is unknown.

A great many characters, useful at a number of taxonomic levels, are found in the median lobe of gyrophaenines. These modifications are too varied to discuss in detail here. They are considered further in the generic descriptions. In general, the apical process is very long and slender (Figure 197), blade-like (Figure 203), highly complex (Figure 193) or has many other modifications. The basal portion is variously modified, and the flagellum is tubular (Figure 192), very long and whip-like (Figure 197) or sclerotized and complex (Figure 194).

Parameres: Parameres (Figure 6) are composed of three sclerites: the condylite (con.), the paramerite (par.), and the apical lobe of the paramerite (ap.l.).

The condylite is a relativley slender structure which articulates with the paramere condyles of the median lobe. The paramerite articulates with the condylite near the apex of the latter. The proximal 1/2 to 1/3 of the paramerite bears more or less markedly sclerotized phragmata internally for muscle attachment. In most, the distal portion of the paramerite is delimited from the basal portion by a less sclerotized "hinge zone" (h.z.). Distally the paramerite bears two independently mobile structures, the apical lobe of the paramerite (ap.l.) and the velar sac (v.s.). The apical lobe of the paramerite of most gyrophaenines is filiform and bears 4 large setae. Size and shape of the apical lobe and relative placement and development of the setae provide characters useful at a number of taxonomic levels. In some, the apical areas of the paramerite and the apical lobe have a number of sensory or glandular pores. The oblique row of pores on the apical area of the paramerite is particularly distinctive of gyrophaenines (Figure 218 and others), though not limited to this group.

A submembranous velar sac is a unique element of the paramere of aleocharines. The velum is a complex structure made up of contributions from both the condylite and the paramerite. The velar sac is probably sensory or adhesive and is distended by increasing hydrostatic pressure.

Among gyrophaenines, a number of useful character systems are found in the parameres. These include: variation in size and shape of apical lobe of paramerite; differences in size and placement of setae of apical lobe; differences in position and development of phragmata; and others. These are discussed more fully within the generic descriptions.

## 3.1.2 Natural History

### 3.1.2.1 Habitat

#### 3.1.2.1.1 General Distribution

As far as is known, all gyrophaenines are obligatory inhabitants of fresh fruiting bodies of gilled and polypore mushrooms as both larvae and adults. However, as discussed more fully later (Section 5.4.2), gyrophaenines are seldom encountered on many groups of fungi producing fruiting bodies commonly called "mushrooms". Adults colonize mushrooms soon after spore producing tissue is exposed, and both larvae and adults are found on more mature mushrooms. Both adults and larvae feed exclusively by "grazing" on the spore producing layer (the hymenium). Because of this requirement for an active hymenium layer, gyrophaenines inhabit only fresh mushrooms. By the time the mushroom begins to decay all gyrophaenines (both larvae and adults) have usually left.

Adults and larvae of those gyrophaenines which live on gilled mushrooms are in spaces between the gills. They are almost never on the cap, stem, base or other parts of the mushroom, and they do not burrow into the flesh of the mushroom.

Adults and larvae of those species which normally live on polypore mushrooms are usually found on the pore surface. Pores of many polypores are too small to admit the beetles. However, some polypores have larger pores (e.g. *Daedalea* and related mushrooms), and both larvae and adults are commonly found in the pore tubes or sinuations.

Because of the apparent affinity of gyrophaenines for tight places, both larvae and adults of those species on polypores often take refuge from the exposed pore surface in cracks, crevasses, holes due to insect damage, and under bits of bark at the base of the mushroom.

Occasionally adults and very rarely larvae are found under or in logs, especially if fungus covered, or in leaf litter at the base of logs. Adults may also be found in moist or moldy leaf litter or in leaf litter beneath mushrooms.

Specimens of some genera (*Brachida*, *Encephalus*) are not commonly found on mushrooms. Little is known about habits of members of these genera. *Brachida exigua* (Heer) is collected in Europe most commonly from grass tufts and ground litter (Lohse, 1974), but Benick (1952) reports it from a tree-fungus. *Encephalus complicans* (Westw.) is commonly collected in hay and rotting grass, often in bogs (Lohse, 1974).

No habitat information is available for specimens of *Probrachida*. I have collected 2 specimens at light, and I have seen 1 specimen from "moist litter". Unfortunately, Sharp (1883) did not provide collecting data for members of this genus.

Cameron (1939) reported *Adelarthra barbari* from "rotten log" and "in log with ants". Label data from the 2 known specimens of this species are "debris" and "wood (rotten)". These may have been associated with fungus (probably polypores) on the logs. An obligatory or facultative association with ants seems unlikely.

Gyrophaenines are rarely found on rotting fruit or by sweeping vegetation. These are almost certainly atypical habitats for these insects.

#### 3.1.2.1.2 Aggregation of gyrophaenines

Adults, and, on more mature mushrooms, larvae, are commonly found in very large numbers on mushrooms. For example, in one collection more than 750 individual adult gyrophaenines were collected from a single fruiting body of *Amanita verna* (Fr.) Quel. While this large number of individuals per mushroom is exceptional, it is common to find tens of individuals per mushroom, and not unusual to find 100 or more individuals per mushroom.

Fenyes (1918) (after Ganglbauer) stated that specimens of *Gyrophaena* form "colonies" on gilled mushrooms. This may be taken to imply some sort of societal organization and is misleading. Gyrophaenines are opportunists and are simply attracted individually to fresh mushrooms where they form aggregations.

There is, however, some evidence that gyrophaenines may be gregarious. In many groups of mushrooms of the same species, one or a few of the fruiting bodies have large concentrations of gyrophaenines, while others have few or none of these beetles on them. In addition, on a single collecting trip many fruiting bodies of a species of mushroom may be sampled which produce few or no gyrophaenines, then a specimen will be found on which gyrophaenines are concentrated in large numbers. This suggests that gyrophaenines may be actively aggregating. A possible aggregation mechanism might be use of pheromones. Such aggregation pheromones have been hypothesized for fungus beetles of the family Ciidae (Lawrence, 1973).

Advantages of aggregation might include increased contact and subsequently better mating success, and perhaps surety of being attracted to a mushroom already found to be a suitable host by other gyrophaenines. There are, however, other possible explanations (other than active aggregation) for these discontinuous distributions. These include undetected differences in age or physiological condition of the mushroom and possibly chance (random) effects such as a fruiting body developing near a previous concentration of gyrophaenines (*e.g.*, a concentration of larvae which emerge to adults, overwinter concentration, concentration of adults leaving a nearby previously occupied mushroom, *etc.*).

### 3.1.2.1.3 Feeding Habits

All gyrophaenines appear to be totally mycophagous as both larvae and adults. There is no indication that they are predaceous (even facultatively) at any stage of the life cycle. Both larvae and adults "graze" maturing spores, basidia, cystidea and hyphae from the hymenium layer of the mushroom. White (1977) reports that feeding activities of gyrophaenines leave "broad lines over the gill surface where spores and basidia are absent" (p.307). My own observations concur.

Maxillae of gyrophaenines appear to be the main feeding structure. They are strikingly modified for "grazing" on the hymenium layer of mushrooms (see Section 5.3.1.1), rapidly scraping the hymenium as the beetle feeds. The mandibles usually also work at the same time as the maxillae. However, grazing movements by the maxillae are often observed without corresponding movements of the mandibles.

Function of the mandibles is unclear. They are not highly modified for fungus feeding. They could serve as a shearing device, but this seems unlikely since they are above the maxillae in relation to the hymenial surface. They may also scrape the collected fungus material from the spore brush of the maxillae and form it into a bolus. Seevers (1978) noted that all bolitocharines have a molar region on the inner face of the mandibles beset with rows of small denticles. He suggested that this is an adaptation for eating hyphae and spores of fungi. All Gyrophaenina have well developed rows of small teeth on the molar region. This region of the mandible possibly grinds spores and hyphae grazed from the hymenium. However, whole mount slide preparations of many species of gyrophaenines indicate that in normal position, the molar surfaces of the mandibles are quite distant from each other, and probably cannot grind against one another. It remains possible that these surfaces grind food against ridges on the epipharynx. In this regard, it is interesting to note that while the maxillae of gyrophaenine larvae are remarkably like those of adults, the mandibles are much simpler and lack a molar surface. Therefore, although larvae appear to be scraping the hymenium in a way similar to that of adults, they apparently do not have to subsequently grind the material thus obtained.

Those gyrophaenines which live exclusively on polypore fungi often cannot get into the pores of the mushroom to feed directly on the hymenial layer. Therefore, they may have a fundamentally different feeding activity than the hymenium "grazing" of those gyrophaenines which live on gilled mushrooms, or those which live on polypores with large pores. I have not observed feeding activity of gyrophaenines on polypores with very small pores, nor has this been described in the literature. It seems likely that larvae and adults of these beetles simply graze the maturing spores, hyphae and basidia which protrude from the pore mouths. This is suggested by examination of gut contents of larvae of *Agaricomorpha apachaena* (Seevers). Larvae and adults of this species live in *Fomes* species in the southwestern U.S. Fruiting bodies of this fungus have very tiny pores. Guts of these larvae were filled with a mixture of mature fungus spores, broken cells, and masses of hyphae. Interestingly, those gyrophaenines which live on woody polypore mushrooms have a lacinial spore brush with relatively more numerous, closely spaced, shorter teeth (in comparison to those which live on gilled mushrooms). This spore brush structure is probably in some way related to requirements of feeding on woody polypores (see Section 5.3.1.2).

### 3.1.2.2 Life History

#### 3.1.2.2.1 Diel Activity Patterns

Very little is known about the daily activity patterns of gyrophaenines, and virtually nothing has been published on this aspect of gyrophaenine natural history. However, some circumstantial evidence seems to indicate that gyrophaenines are mostly diurnal.

Ashe (1981a) reports colonization of mushrooms by adults of *Phanerota fasciata* (Say) late in the afternoon. In addition, I have observed instances of colonization of mushrooms by various species of *Gyrophaena*. All were during the day and most were mid- to late afternoon. These observations, though, may only reflect a temporal collecting bias.

All gyrophaenine species have well developed eyes (particularly large in *Phanerota* species). This suggests that vision plays a role in orientation to, or colonization of, mushrooms. While it is true that a few gyrophaenines are found at lights, they are not abundant there, and certainly gyrophaenines do not form part of the typical assemblage of staphylinids found at lights. This suggests that gyrophaenines do not have major periods of dispersal at dusk or during evening, characteristic of many staphylinids – in particular those which live in many other temporary habitats.

Feeding by larvae and both mating and feeding by adult gyrophaenines have been observed numerous times on mushrooms during daylight hours. I do not know if these activities continue during periods of darkness. However, rapid growth of gyrophaenine larvae, especially the very short duration of instars I and II (see below), suggests that feeding may be almost constant, at least during early stages. Continuous feeding activity may be a requirement of those species which live on rapidly decaying gilled mushrooms. Nothing is known of activity patterns of those gyrophaenines which live on more persistent polypore mushrooms. However, the requirement for rapid larval development may be less stringent in these habitats, and this may in turn affect the diel activity patterns of larvae of those species which occur there.

In addition, several instances in which ecdysis from instar I to II or instar II to III occurred during periods of darkness are known (personal observations) further suggesting that activity may be continuous.

In summary, although there is little direct observation of daily activity of gyrophaenines, circumstantial evidence suggests the following may be characteristic. Adults are predominately diurnal, and dispersal and colonization of fresh mushrooms occurs during the day. However, sporadic adult activity may occur at night. Larval activity may be virtually continuous throughout a 24 hour period, but this may vary according to the specific mushroom habitat used.

### 3.1.2.2.2 Life Cycle and Seasonal Activity

In comparison to the marked diversity of gyrophaenines little detailed information about life history and seasonal activity is available. Much must be inferred from circumstantial evidence. The only detailed study of life history of a gyrophaenine was about *Phanerota fasciata* (Say) (Ashe, 1981a). Because of this study, natural history of those species which live on gilled mushrooms is better known. Great opportunity exists for life history studies within the gyrophaenines. Ashe (1981a) emphasized the ease with which these may be done.

#### 3.1.2.2.2.1 Colonization of mushrooms

Because adults mate, lay eggs and feed, and larvae mature on a mushroom before it rots, ability to find and colonize young fresh fruiting bodies is of vital importance to gyrophaenines. Adult gyrophaenines are often among the first insects to colonize fresh mushrooms, and are often found in gilled mushrooms soon after the gills are exposed. Colonization apparently occurs by adults flying to the fresh mushrooms. Ashe (1981a) reports adults of *Phanerota fasciata* flew over the mushroom, landed on the cap, then ran around to the undersides. I have observed similar activity by members of other species.

It is not known how gyrophaenines find mushrooms. However, mushrooms produce a variety of volatile chemicals, and it is reasonable to expect that at least part of the attraction of gyrophaenines to mushrooms is an olfactory response to these chemicals.

Gyrophaenines may make the decision about whether a mushroom is a suitable host before or after arriving on the mushroom. Adults may respond only to mushrooms with certain chemical and physical characteristics. On the other hand, gyrophaenines may be attracted to a wide variety of mushrooms and accept or reject each as a host after exploratory feeding or other activities on the mushroom. It is most likely that both of these are factors in host choice.

Although the mechanism of host finding by gyrophaenines is unknown, it is, as indicated above, apparently quite efficent.

### 3.1.2.2.2.2 Mating

I have observed mating by gyrophaenines including *P. fasciata* (Ashe 1981a) on both polypores and gilled mushrooms, and surmise that mating normally occurs on the mushroom.

Mating by members of *P. fasciata* is similar to that described for *Aleochara curtula* by Peschke (1976). The male bends the abdomen forward over his dorsum, extrudes the aedeagus and attempts to make contact with the female's abdomen. If contact is effected, the median lobe of the aedeagus is inserted into the genital chamber of the female and copulation is initiated. Among most aleocharines which use this mating position male and female may face in the same direction with the male slightly behind and to one side of the female. This orientation is commonly found among gyrophaenines. However, among those which occur in gilled mushrooms, a slightly different mating configuration is often observed. After copulation is initiated as described above, the male may straighten his abdomen and take a position on the mushroom gill facing the one the female is on. In this position the bodies of the male and female form an angle of 180° to each other, face in opposite directions, and each is upside down in relation to the other. This position has been described in *P. fasciata* (Ashe, 1981a) and I observed it in a number of species of *Gyrophaena* which live in gilled mushrooms.

This position is a relatively simple modification of the "typical" mating orientation and is probably limited to those species which occur on gilled mushrooms or similar habitats in which two closely opposing surfaces are available for members of a mating pair to stand on.

It is not known whether females must mate on each mushroom before egg laying is initiated, or whether females previously mated on another mushroom can begin egg laying activities immediately after colonization of a mushroom. This is important, especially for those species which live on gilled mushrooms, since the relatively short life of many gilled mushrooms may place severe constraints on time available for completion of life cycles.

### 3.1.2.2.2.3 Oviposition and eggs

Observations of oviposition by gyrophaenines have not been published. I have not observed this process, nor have I observed eggs of those species which live on polypores. Therefore, these comments are limited to those species which occur on gilled mushrooms. It is reasonable to assume that egg laying will be similar in those species which occur on polypores, but this remains to be verified.

Ashe (1981a) reported finding eggs of *P. fasciata* on specimens of a species of *Russula* (prob. *R.foetans* (D.C. ex

Fr.). The eggs were arranged in loose irregular clusters of 4 to 14 on the surface of the gills "with the long axis of the egg parallel to the gill surface." These eggs were ovoid, white, translucent, and measured 0.39 × 0.43 mm.

I have also observed eggs of *Gyrophaena (Phenogyra) californica* Csy. on a species of *Paxillus*. These eggs are similar to those of *P. fasciata* and were also found in loose clusters on the gills. These, however, were also found in loose rows at the base of the gills. Larvae hatched from the eggs of both species. Larvae from eggs of *P. fasciata* were reared to adults.

These observations are in contrast to those of White (1977), who reports finding eggs of *Gyrophaena gentilis* Erichson "laid singly into the proximal margin of the gills of *Tricholmopsis rutilans* (Fr.) Sing." (p.307). This seems to imply that eggs are inserted individually into the gill margin near the base. This is different from egg positioning described above. This discrepancy cannot be reconciled at this time. However, White does not actually report having observed these eggs hatch into gyrophaenines. Also, since gyrophaenine females lack a sclerotized ovipositor, it is not clear how the eggs are inserted into the gill flesh.

Topp (1975) reported that adult females of *Bolitochara lunulata* Payk. and *Aleochara moerens* Gyll. take their eggs in their mandibles immediately after oviposition and deposit them in a suitable hiding place. Later (1977) he reported a similar activity among females of several athetine species and suggested that this may be a characteristic habit of aleocharines. It is not known if females of gyrophaenine species rearrange their eggs after oviposition.

Oviposition probably occurs very soon after colonization. Supporting this suggestion is the fact that Ashe (1981a) found eggs of *P. fasciata* on a mushroom which was being colonized. However, circustantial observations made while retaining adults with fresh mushrooms suggest that there may often be a longer pre-oviposition period after colonization.

#### 3.1.2.2.2.4 Eclosion

Ashe (1981a) has described eclosion in larvae of *P. fasciata*. Quick, jerking movements were observed within the chorion as early as an hour before eclosion. Eclosion is effected when the larva straightens its body and splits the chorion at the head end. The larva crawls free and the chorion collapses. Egg bursters have not been observed in instar I larvae of gyrophaenines. Ashe (1981a) suggested that small teeth on the outer surface of the mandibles of instar I larvae of *P. fasciata* may serve to abrade the inner surface of the chorion during the quick, jerking movements which proceed eclosion.

Ashe (1981a) reported that larvae of *P. fasciata* begin feeding immediately, often before completely free of the chorion. This rapid initiation of feeding activity after eclosion is probably typical of gyrophaenines which live on gilled mushrooms.

Based on circumstantial evidence, Ashe suggested that the incubation period of eggs of *P. fasciata* is about 24 hours at room temperature (22-24°C). The mushroom was being colonized at the time of collection, suggesting that adults had not been on the mushroom long. All eggs hatched at very nearly the same time, and all eggs had hatched within 22 hours of collection. Eggs of most other gyrophaenines which occur on gilled mushrooms probably have incubation times which do not vary greatly from this.

#### 3.1.2.2.2.5 Growth and development of larvae

Growth and development of gyrophaenine larvae is very rapid. Again, the only detailed data available for larval development are for *P. fasciata*. However, my observations incidental to rearing a number of species of *Gyrophaena* indicate that developmental times reported for *P. fasciata* are very similar to those of many other gyrophaenines – at least those which occur on gilled mushrooms.

Gyrophaenines have 3 larval instars. At room temperature larvae of *P. fasciata* completed instar I in an average of 14.2 hours, instar II in 14.8 hours and instar III (to the time the larva left the mushroom) in about 2 days. Thus the entire larval period on the mushroom occupied only about 3 days with the first 2 instars completed in about a day.

When instar III larvae are mature (at the end of about 3 days of larval life), they become restless and begin to crawl away from the mushrooms. These larvae push their way into cracks or interstices of the litter and soil and begin to form pupal cells.

While observations indicate that this description of larval development is true for most species which occur on gilled mushrooms, it is not known whether it also applies to larvae of those gyrophaenines which live on polypore mushrooms. The greater longevity of polypores, the fact that they do not produce spores in this abundance over such a short period of time as do gilled mushrooms, and the fact that polypores may produce spores sporadically rather than continuously, may seriously affect rates of larval development. Larvae of gyrophaenines which live on polypores may require much longer to develop than those which live on gilled mushrooms.

### 3.1.2.2.2.6 Pupal cell formation and pupation

Pupal cell formation begins soon after a larva crawls into the soil.

Construction of pupal cells by larvae of *Gyrophaena nana* Payk. has been described by Ashe (1981b). After selection of a space between substrate particles, a larva begins to enlarge and shape it by rearrangement of the substrate particles with its mandibles. Silk is extruded as a clear, colorless droplet at the apex of the abdomen. This droplet is touched to the substrate and drawn out as a thin thread. Silken threads are used to bind substrate particles in position. Completion of the pupal cell requires 12-24 hours.

The completed pupal cell is ovoid or spheroid and consists of a mass of substrate particles held together by a loose to dense network of fine silk fibers. The center of this cell is occupied by a more or less densely woven coccoon within which the larva pupates. Pupal cells constructed in this way are probably typical of most aleocharines. After completion of the pupal cell the larva becomes inactive and shortens and thickens to form a prepupa. Ecdysis to the pupa occurs 2-3 days later.

Duration of the pupal stage varied from 8-12 days for *P. fasciata*, but I have observed pupal stages as short as 5 days (*Gyrophaena nana*) and as long as 14 days (several species).

After ecdysis, most teneral adults remain in the pupal cell 1-2 days before emerging from the soil. Many adults are still teneral when they emerge from the soil, but are quite active and able to fly well even though sclerotization is incomplete. Probably these newly emerged adults colonize fresh mushrooms immediately if these are available. Teneral adults are fairly common on fresh mushrooms in late summer. However, they may become semidormant in leaf litter or under logs if fresh mushrooms are not available.

Because generation time is short, and newly emerged adults can immediately colonize fresh mushrooms, more than one generation per year is possible. Batten (1973) reported that *Gyrophaena gentilis* Erichson is bivoltine in Holland.

I do not know if number of generations per year is genetically determined for each species, or if number of generations per year is indeterminate and varies with length and climate of the growing season and with length of time fresh mushrooms are available.

While the above summary of a probable multivoltine life history seems correct for most species of *Gyrophaena*, some may be obligatorily univoltine. A number of my attempts to rear larvae of several species of the *Gyrophaena pulchella* species group (Seevers, 1951) have failed. Mature larvae of members of this group burrow into the soil and form pupal cells. However, I have not been able to get them to complete development to pupae. Larvae simply remain in pupal cells until they die 1-2 weeks later, which suggests that some essential requirement for pupation is not being supplied. This contrasts sharply with the ease with which other species of *Gyrophaena* have been reared. While other hypotheses are possible, at present the most simple explanation for these observations is that members of the *G. pulchella* group require a diapause period, probably cold induced, to initiate pupation and subsequent development. If this is true then they are probably univoltine. While the hypothesis that members of the *G. pulchella* group are obligatorily univoltine requires comfirmation, it suggests that other species of gyrophaenines may also have only a single generation per year.

### 3.1.2.2.2.7 Seasonal activity

Seasonal activity patterns of gyrophaenines are determined chiefly by fruiting cycles of mushrooms. In general, gyrophaenines may be active throughout the summer and early fall whenever mushrooms occur. However, individual species may have more restricted periods of activity, which for at least some species, seem to correspond primarily to appearance of a particular assemblage of mushrooms, probably including preferred host(s) of that species.

A particularly striking example of a restricted period of activity is illustrated by two years of observations of the habits of *Gyrophaena simulans* Csy. near College Station, Texas. In this area mushrooms are common from late spring until late fall following periods of wet weather. Gyrophaenines are found on mushrooms any time fruiting bodies occur, with specimens of most species present throughout the fruiting season. During the two seasons that I collected around College Station, adult specimens of *G. simulans* were very rarely encountered during most of the fruiting season. However, in mid to late October, adults of this species began to appear in abundance on fruiting bodies of *Tricholoma* (prob. *T. sulfureum* Fries) which first fruited at that time. A large number of adults and larvae of *G. simulans* were found throughout the fruiting period of this mushroom. With cessation of fruiting of this species of *Tricholoma*, *G. simulans* virtually disappeared from the gyrophaenine fauna until the next October. Even during the time of maximum beetle activity, adults of *G. simulans* were seldom encountered on other mushrooms, at least in the College Station area. It is important to note that *G. simulans* occurs throughout the eastern United States. In most other areas it colonizes a much broader range of mushrooms than was observed in the study area. Consequently, in most areas, its seasonal activity period may be much longer.

Such apparent restricted periods of activity may reflect a collecting bias. However, this is almost certainly not always true, and a more or less seasonally restricted activity period seems to be the rule for a number of species of gyrophaenines.

As noted for *G. simulans* above, seasonal activity pattern for a species may vary geographically.

Mushrooms are often not present throughout the time when most gyrophaenine species are potentially active. Absence of fruiting bodies is especially apparent during dry periods. It is uncertain how the beetles respond to this situation. Few adults are found in moist or moldy leaf litter or under logs during these periods. It seems likely that when suitable hosts are not available, adults enter the litter and become semidormant.

Because of the marked behavioral and morphological adaptations of gyrophaenines to feeding on the hymenium layer of mushrooms, it is unlikely that most of these beetles feed on fungus mycelium when they are found in moldy leaf litter or under fungus covered logs. This may not be true of those, such as species of *Encephalus* and *Brachida*, which appear to be normally found in these habitats.

It is not known how gyrophaenines coordinate their periods of activity to times when mushrooms are present. Most probably avoid the problem of very exact timing of adult activity by having a range of host preferences rather than being highly adapted to a single mushroom species. They may simply periodically search for mushrooms then become inactive again if suitable mushrooms are not found. On the other hand, they may become active in response to environmental cues. Since many fungi commonly form fruiting bodies following periods of wet weather, increase in moisture is a possible general cue for gyrophaenines to become active. Many gyrophaenines may profitably occupy a range of different mushrooms, so that such general cues may be sufficient. However, many mushrooms are quite seasonal in occurrence. Those species of gyrophaenines which have a restricted range of host preferences may require more specific cues to allow timing of activity periods to the proper season.

### 3.1.2.2.2.8 Discussion of life cycle

Evolution of ability to eat maturing spores, basidia and cystidea of the hymenium layer is a major evolutionary innovation for gyrophaenines. This ability opened a new adaptive zone within the mushroom habitat which provided an abundant and virtually unexploited, but highly unpredictable resource. However, the requirement for a fresh and active hymenium layer for both larval and adult survival imposes a number of constraints on the life history of gyrophaenines. Many of the features of the life cycle are a response to the unique characteristics of the mushroom as a habitat.

For gyrophaenines the most important general characteristics of the mushroom habitat are that mushrooms are: 1) ephemeral (often highly so); 2) unpredictable in time and space; and 3) highly heterogenous in physical and chemical characteristics. Exploitation of habitats with these characteristics requires adaptation to: 1) an efficient host finding mechanism; 2) rapid larval development; and 3) some means of surviving when suitable mushrooms are not available.

Because both adults and larvae of gyrophaenines probably feed exclusively on the active hymenium layer of mushrooms, they occur only on fresh mushrooms. Decaying mushrooms are not suitable habitats for these beetles and are soon colonized by other species of staphylinids which are probably predaceous. Among mushrooms inhabited by gyrophaenines, time from first spore production until the mushroom becomes unsuitable as a habitat varies considerably depending on a number of factors including particular species of mushroom; temperature, humidity and rainfall; and how extensively the mushroom is attacked by other insects, particularly fly larvae. The period that a mushroom remains a suitable habitat for gyrophaenines may vary from as little as a week for some gilled mushrooms to a month or more for woody polypores.

Mating, oviposition and larval development must take place on a single mushroom. Apparently larvae leave the mushroom only to pupate. It is unlikely that any larvae survive if the mushroom which they inhabit is destroyed or decays before they are mature.

This is a serious constraint, especially for those gyrophaenines which occupy short-lived gilled mushrooms. Efficient host finding, rapid colonization and oviposition, short incubation period of eggs and very rapid larval development are undoubtedly adaptations to the ephemeral nature of these mushrooms.

However, in many characteristics which are important to gyrophaenines, gilled and polypore mushrooms are quite different habitats. Unfortunately, as noted above, no details are known of the life history of those gyrophaenines which occur on polypore mushrooms. However, at least potentially, responses to the different conditions of these two major mushroom types could produce marked differences in the life cycle and population structure of the gyrophaenines which occupy them.

One of the most obvious differences between the two types of mushrooms is length of time that each is present in the environment. Gilled mushrooms are commonly short-lived, many decaying within a few days to a week. In contrast, polypores, especially woody species may persist for several weeks to a month or more. It seems reasonable to expect that those gyrophaenines which live on persistent polypores are under less stringent requirements for a very rapid life cycle than those which live on gilled mushrooms.

Another potentially important difference is availability and production rate of hymenium tissue of the two groups of mushrooms. Gilled mushrooms have a very active hymenium layer, producing great quantities of spores during a relatively short period of time. Since the hymenium layer is on the surface of the gills, and the gyrophaenines actually live between the gills, the beetles have an abundance of readily available food constantly throughout the life cycle. The hymenium layer of polypores, on the other hand, is formed inside pores many of which are too small for a beetle to enter. Also, polypores produce spores for a much longer period, though spore production throughout this period may not be constant. Many polypores produce spores periodically, often in response to wet weather. This periodic production of spores and relative isolation of beetles from direct contact with the hymenium layer may have effects on both life cycle and feeding habits of members of those species which inhabit polypores.

Possibly, gyrophaenines which habitually live on more persistent woody polypores may colonize more slowly, mate and oviposit for a more extended period, have a longer larval period, and have adults and larvae overlapping occupancy of the same mushroom for a more extended period. Observations about natural history of those gyrophaenines which are obligatory inhabitants of persistent polypores are required to test these suppositions.

Polypores may not be as productive a habitat as are gilled mushrooms, because one seldom finds very large numbers of individual beetles per mushroom on persistent polypores.

An interesting possibility is that feeding and life cycle requirements imposed on gyrophaenines by the extremes of these two general types of mushroom habitats makes it difficult for beetles to change from one type to the other. Thus the broad host trends displayed by members of gyrophaenine taxa which are restricted to either polypores or gilled mushrooms respectively may be reinforced by the difficulty which members adapted to one group experience in surviving on the other.

Although differences in general habitat features between persistent polypores and very emphemeral gilled mushrooms are quite striking, these extremes are connected by a range of habitats of more or less short-lived polypores and more or less persistent gilled mushrooms. Mushrooms which exhibit intermediate general characteristics provide a bridge or "transition zone" (Bock 1965) of habitats between these two extremes. This transition zone has probably been very important in evolution and diversification of gyrophaenines in the various mushroom groups.

### 3.1.2.3 Interactions with other mushroom-inhabiting insects

Detailed observations have not been published about how gyrophaenines interact with other insects which occupy mushrooms. However, several interesting hypotheses about the broad, general characteristics of these interactions can be inferred from a comparison of the ways that gyrophaenines and other insects use the mushroom habitat.

Evolution of the ability to feed exclusively on the spore producing tissues of mushrooms is the key innovation which opened the mushroom habitat to gyrophaenines. This particular way of using mushrooms fundamentally affects relationships with other mushroom-inhabiting insects.

The habit of eating mushroom spores is limited to a few groups of relatively small insects and includes ptiliid beetles (subfamily Nanosellinae, Dybas 1976), some Collembola, and members of some families of Acarina. Lawrence and Newton (1981) discuss many groups of insects which eat spores and fruiting bodies of slime molds (Myxomycetes).

Gyrophaenines differ from other insects which eat spore tissue in that they are relatively large (in relation to the tissue they consume), and they do not eat only mature spores. Instead, they are capable of feeding on both maturing spores and also the hyphal structures of the hymenium layer of gilled and polypore mushrooms. Therefore, gyrophaenines eat both spores and spore producing tissue.

In addition, most arthropods which inhabit mushrooms eat, not the hymenium layer, but the context tissue of gills, caps or stems.

Thus, it appears that there is little direct competition for this food resource within the mushroom habitat. However, because of the large number of animals, particularly arthropods, which use mushrooms, indirect competition may be very important to gyrophaenines. Any animal whose activities reduce or destroy the ability of a mushroom to produce a hymenium layer is in indirect competition with gyrophaenines.

A number of arthropods eat the flesh of the gills, or the context of the cap. These include larvae and adults of several species of erotylid beetles (including *Triplax* Hbst. and *Tritoma* Fab. species) (Arnett 1968), both adults and larvae of some scaphidiid beetles (Arnett 1968, and personal observations), *Oxyporus* Fab. adults and larvae (Campbell 1969, and personal observations), and some nitidulid beetles (Arnett 1968). Activities of fly larvae are particularly important in gilled fungi. Large numbers of these burrow in the cap, stem and gills of mushroom extensively damaging the mushroom, especially as larvae begin to mature. In addition, some slugs often feed on the gills and caps of mushrooms. Even if feeding activities of an animal on the mushroom do not directly affect the gills, the trauma caused to the mushroom tissue may accelerate rotting of the fruiting body. Scheerpelz and Höfler (1948) pointed out the dramatic hastening of rot caused by feeding activities of fly larvae within caps of gilled mushrooms.

In general, activities of other arthropods on polypores are probably of less importance to gyrophaenines than on gilled mushrooms. However, feeding on the pore surface may reduce the reproductive capability of a polypore. Adults of some erotylid beetles, such as members of *Dacne* Latr. and *Megalodacne* Crotch (personal observations) feed extensively on the pore surface, while larvae burrow into the pore layer. Some scaphidiid and tenebrionid beetles have similar habits. Slugs may also be important in destruction of the pore surface at certain times. Other beetles (and in softer polypores, fly larvae) may bury into the context of the fruiting body, ultimately destroying it. These include, most importantly, tenebrionid beetles such as *Bolitotherus cornutus* (Panzer) and *Diaperus maculata* Oliver.

Many important inhabitants of polypores, such as ciid beetles, generally colonize fruiting bodies after spore production has ceased (Lawrence, 1973; Pavoir-Smith, 1960) and probably have little effect on gyrophaenines.

Since gyrophaenines usually colonize a mushroom very soon after spore production begins (at least for those that live on gilled mushrooms), they probably normally avoid interaction with many of the predaceaous and saprophytic beetles (mainly staphylinids) which colonize the later stages of fruiting bodies. The presence of late instar gyrophaenine larvae may overlap colonization of mushrooms by these later inhabitants, so it is possible that gyrophaenine larvae may be preyed upon by these predators. However, this predation has not been observed. It would be very surprising if gyrophaenine larvae do not form a food source for some predators, since they may be very abundant on more mature mushrooms. In this regard, the very well developed glandular process on tergum 8 of gyrophaenine larvae may be important. Moore, Legner and Badgley (1975) showed that a similar gland in larvae of *Oligota oviformis* Csy. acted as an osmeterium and suggested that it may have a defensive function. Use of the tergal gland has not been investigated in gyrophaenine larvae.

## 3.2 Perspectives on Classification

Development of a general purpose classification of organisms is one of the most important tasks of systematists. Several recent works (Eldredge and Cracraft 1980; Wiley 1981; Mayr 1981; and included references) have discussed in detail the philosophical, methodological and historical base of biological classifications. These need not be reviewed in detail here.

I agree with Mayr (1981) that a classification must serve as a basis for an information and retrieval system, and also as a basis for biological generalizations. Most systematists agree that a classification based on evolutionary patterns is most convenient for biological organisms. In order to most completely meet these requirements, as much evolutionary information as possible should be included in the classification. However, Eldredge and Cracraft (1980) have correctly pointed out that if the Linnean hierarchy is used as the system for classification, then the only information actually contained within the structure of the classification itself is the hierarchical arrangement of taxa. This hierarchical structure, then, is the only information which can be extracted from the classification without addition of conventions or explanations. The Linnean hierarchy is particularly suited as a classification system because the geneological structure of taxa is hierarchical. This hierarchical structure of geneological relationships is hypothesized in a cladogram. "Cladistic" classifications transfer information directly and unaltered from a cladogram to a classification, so that each strictly monophyletic group is given a categorical rank in the classification, and the hierarchical structure of the cladogram is directly reflected in hierarchical structure of these categorical ranks. In this system, all evolutionary information (geneology) put into the classification is directly retrievable from the structure of the classification itself.

The major contending classification system is called an "evolutionary" classification. Proponents of this method argue that the most generally useful classification includes not only cladistic (geneological) relationships, but also information on degree of similarity of organisms included in each taxon (patristic relationships). This often leads to recognition of paraphyletic groups within a classification. While paraphyletic groups can contain very useful information, particularly ecological, structural and developmental similarity of included taxa, addition of such information to a classification results in loss of geneological information. That is, since hierarchical structure is the only information inherent in the classification, the geneological relationship between the paraphyletic group and the monophyletic group derived from it cannot be recognized. Additionally, if both patristic and cladistic relationships are included, then it becomes impossible to determine which is being reflected at any one point in the classification. Finally, since patristic relationships are not hierarchical in the same sense that geneological relationships are, patristic relationships cannot be suitably reflected by the hierarchical structure of the Linnean system. Despite these problems with evolutionary classification, there are times when information about patristic relationships are more valuable for comparison than is information about geneological relationships.

Because of the nature of the Linnean hierarchy itself, I prefer a classification which is cladistic in that all included taxa are strictly monophyletic. Patristic information can be expressed by convention or explanation of taxa within the classification.

In addition to the uses of a classification mentioned above, a classification must act as a vehicle for communication of information about organisms. To perform this function a classification must have a certain amount of stability.

This requirement for effective communication and stability in a classification has been, in part, the reason that I have taken a conservative approach to reclassification of gyrophaenine genera in this treatment. The gyrophaenines are one of the few major groups of aleocharines for which a relatively large number of character state distributions have been analyzed. Analysis of other groups of aleocharines may ultimately result in major changes in character analysis of states in gyrophaenines. It is, therefore, possible that hypotheses about relationships of gyrophaenine genera will require slight to considerable modification. Therefore, I have retained all genus-level names which have been proposed as long as the group can be hypothesized to be monophyletic. This requires that monophyletic lineages of similar external structure be given generic rank, and has resulted, for example, in splitting *Agaricomorpha* n. gen. from *Agaricochara* Kraatz though they are similar externally. This also has resulted in a situation in which the genus-level diversity within taxa of the "Sternotropa" lineage is not much greater than that among species-group level taxa within *Gyrophaena*. The "Sternotropa" lineage may include too many genus-level taxa. Alternatively, *Gyrophaena* is an exceptionally diverse group of organisms, and may include several monophyletic lineages, each of which deserve generic rank.

I believe that proposal of a more rigorous cladistic classification of gyrophaenines, or any large group of aleocharines, is premature at this time. Many changes in classification of aleocharines can be expected as knowledge of relationships increases. Major revisions in classification before other aleocharines are better known are likely to lead to instability and confusion later.

## 3.3 Nomenclature, Description and Identification

### 3.3.1 Description and Reclassification of World Genera of the Subtribe Gyrophaenina

### 3.3.1.1 Subtribe Gyrophaenina

Gyrophaenini (Eurypalpi) Kraatz 1858:352
Gyrophaenides Thomson 1860:266
Gyrophaenae Fauvel 1875:631
Gyrophaenae Casey 1906:275
Gyrophaenae Fenyes 1918:18
Gyrophaenini Fenyes 1921:34
Gyrophaenae Seevers 1951:670
Gyrophaenina Arnett 1968:285
Gyrophaenini Lohse 1974:25
Gyrophaenae Seevers 1978:161

*Diagnostic Combination*. – Adults of subtribe Gyrophaenina are recognized by the combination of nonstyliform labial palp, broadly separated middle coxae, broad meso- and metasternal processes not joined by an isthmus but meeting along a broad suture, truncate lacinial apex with well developed spinose area (spore brush), reduced spines and setae on inner face of lacinia, 4 well separated rows of flattened setae on apex of galea in most, and a plate-like flange on neck of spermatheca.

*Description*. – Body length 0.6 to 3.5 mm. Body form and color various.

*Head.* – Infraorbital carina well developed, complete or reduced antero-laterally. With or without additional carina from dorso-lateral base of neck to gular sutures. Neck absent. Gula with sutures more or less widely separated. Eyes medium sized to very large. Antenna 11-articled. Labrum with major setae well developed, with or without additional setae; medial sensilla area well developed; lateral sensillum row with 3 to 5 sensilla, at or more or less distant from lateral margin, sensilla well developed or reduced. Maxillary palpus 4-articled. Lacinia with apex obliquely truncate with more or less dense patch of teeth (Figure 73); inner face without teeth or spines (in most) or with few scattered teeth, setae in single row (in most) or loosely scattered to moderately dense. Galea with apical setae more or less flattened, in 4 distinct rows (in most), or unmodified and in 5 to 13 rows. Mandibles more or less robust; apices simple, or left, and in some also right, mandible bifid at tip; right mandible with slightly to well developed molar tooth. Prostheca well developed, membranous. Labial palpus 2-articled, not styliform. Ligula various. Medial setae of labium 2, or, in most, 1.

*Thorax.* – Pronotum transverse to broadly rounded; posterior margin bisinuate to broadly rounded. Hypomera visible or not in lateral aspect. Elytral apical angles markedly to not sinuate. Prosternal peritremes behind procoxae absent, procoxal cavities broadly open. Mesosternum with carina complete, incomplete, reduced to low ridge, or non-carinate. Mesosternal process broad, extended between middle coxae to metasternal process along broadly rounded or truncate juncture; juncture suture complete, fused or more or less beaded. Isthmus absent, mesosternal process extended to middle or base of middle coxae. Middle coxae widely separated. Tarsal formula 4-4-5.

*Abdomen.* – Abdominal segments 3 to 7 more or less deeply transversely impressed to 3 to 5 slightly impressed. Tergum 7 with abdominal gland openings on anterior margin.

*Male genitalia.* – Median lobe and parameres varied. Flagellum large, tubular, slightly to moderately sclerotized. Median lobe without complex internal structure of eversible membrane, hooks and spines in most. Apical process extensively modified or not.

*Female genitalia.* – Neck of spermatheca with lateral flange-like plate. Spermatheca simple (Figure 176) or neck elongate distal (Figure 185) or proximal (Figure 179) to lateral flange.

### 3.3.1.2 Larvae

Because structural variation among aleocharine larvae is very inadequately known, it is inappropriate to give a full discription of gyrophaenine larvae at this time. The following diagnosis is given to aid identification.

*Diagnostic Combination*. – Among aleocharine larvae, gyrophaenine larvae are recognized by the obliquely truncate mala with numerous, more or less closely spaced teeth, large, well developed abdominal gland on tergum 8, and the association with fresh mushrooms.

*Discussion* – Few detailed studies of larvae of gyrophaenines have been published. These are discussed under the appropriate genus.

I have examined probable larvae of species representing seven genera of gyrophaenines: *Agaricochara*, *Agaricomorpha*, *Brachycara*, *Eumicrota*, *Gyrophaena*, *Phanerota* and *Pseudoligota*. These larvae have a number of characteristics in common. The mala of the maxilla is truncate and covered with numerous, more or less closely spaced teeth (Figures 240, 242, 243). Number and spacing of these teeth vary considerably among species and genera. Similarity of this structure to the spore brush on the apex of the lacinia of adult gyrophaenines is striking.

In all gyrophaenine larvae examined, the outer apex of the maxilla has a small bifid plate-like structure which forms a cup over the more distal teeth of the mala (Figures 241). Ashe (1981a) suggested that this structure is a modified seta, but with closer examination, it seems more likely to be a scale-like cuticular modification. This interpretation is given support by additional plate-like structures on the apico-lateral side of the mala of larvae of *Brachycara* species (Figure 243) which appear to have been derived in a similar way to the apical bifid plate. This structure may perform a function in larval feeding similar to that of the rows of plate-like setae on the galea of adult gyrophaenines.

Convergence in mouthpart structure between adult and larval gyrophaenines is evidence that adult and larval gyrophaenines are using resources of the mushroom habitat in the same way.

One important difference in mouthpart structure between adult and larval gyrophaenines is that larvae have sickle-shaped mandibles which lack the well developed, toothed molar region of adults. It is not known how this difference affects mandibular function.

Of particular interest is a brush-like seta on each side of the midline dorsally near the apex of the abdominal tergal gland on segment 8 (Figure 232). These were first described by White (1977) in larvae of *Gyrophaena gentilis*. Ashe (1981a) described similar setae in larvae of *Phanerota fasciata* (Say), and pointed out that similar setae were present on tergum 8 of all gyrophaenine larvae which he had examined. However, White (1977) had reported that he was unable to find the setae on larvae of *Agaricochara* species which he had examined. Ashe (1981a) suggested that he over-looked these structures in these species. I have since examined larvae of *Agaricochara laevicollis* Kraatz and identified these setae, which are very small and spatulate rather than brush-like (similar to those of larvae of *Agaricomorpha apachaena*, Figure 244). No similar structures have been described or are known to me in other aleocharine larvae. A reasonable hypothesis is that complex structure of the maxilla of larval gyrophaenines and presence of brush-like setae dorsally on abdominal tergum 8 are uniquely derived with the Gyrophaenina. These character states then, are synapomorphies, and offer further support that the subtribe as here defined is monophyletic.

### 3.3.1.3 Discussion and Reclassification

The subtribe Gyrophaenina has been differently defined and placed at different formal ranks by different authors. The first to recognize these beetles as a distinct group was Kraatz (1858). In his Subdivision II, the Gyrophaenini (Eurypalpi), he recognized three genera: *Encephalus* Westw., *Gyrophaena* Mann., and *Agaricochara* Kr. Thomson (1860-61, 1867) was first to rank it as a subtribe, the Gyrophaenides, and included *Encephalus* and *Gyrophaena*. Fauvel (1875) returned to the arrangement of Kraatz (1858) with the Gyrophaenae as Section II of the Aleocharinae. Within the Gyrophaenae he included *Gyrophaena*, *Encephalus* and *Brachida* M. and Rey.

Casey (1906) recognized eight genera in the subtribe Gyrophaenae, including, in addition to all genera previously recognized, *Diestota* Rey, *Phenogyra* M. et Rey, and two new genera, *Eumicrota* Csy. and *Phanerota* Csy. Fenyes (1918) recognized seven genera in his "Group Gyrophaenae". He did not include *Diestota* and ranked *Phanerota*, *Eumicrota* and *Phenogyra* as subgenera of *Gyrophaena*. He also included *Brachycara* Sharp, *Haplomicra* Sharp and *Hygroptera* Motsch.

Increase in number of genera in the subtribe continued until Scheerpeltz (1926, 1934) listed 23 genera within subtribe Gyrophaenae. Seevers (1951) was more conservative and recognized only *Gyrophaena*, *Phanerota*, *Encephalus* and *Brachida* within the Holarctic fauna. He ranked *Eumicrota* and *Agaricochara* as subgenera of *Gyrophaena*, but later (1978) recognized these as distinct genera.

Many major workers on aleocharines have not placed these beetles in a distinct subtribe, but have included them within the tribe Bolitocharini or its equivalent. These include Mulsant and Rey (1871-75), Sharp (1883-87), Gangelbauer (1895) and Cameron (1920, 1939).

In this revision I recognize 13 genera in the subtribe Gyrophaenina. These are:

*Gyrophaena* Mannerheim, 1830
*Phanerota* Casey, 1906
*Eumicrota* Casey, 1906
*Encephalus* Kirby, 1832
*Probrachida* new genus
*Brachida* Musant and Rey 1872
*Agaricochara* Kraatz, 1856
*Sternotropa* Cameron, 1920
*Pseudoligota* Cameron, 1920
*Neobrachida* Cameron, 1920
*Adelarthra* Cameron, 1920
*Agaricomorpha* new genus
*Brachycara* Sharp 1883

Members of these genera are similar in a number of characteristics. I believe that two of these, maxillary structure and a plate-like flange on the neck of the spermatheca, provide evidence for monophyly (see Section 4.2.2.4 for discussion).

The reasons for proposing subtribal rank include the conservative approach to classification of aleocharines in accordance with the discussion in Section 3.3. Also, it helps to indicate that the Gyrophaenina is probably a part of a monophyletic lineage of several similarly monophyletic "subtribes" within the tribe Bolitocharini. Evidence for this is the proposed sister group relationship of the Gyrophaenina with the subtribe Bolitocharina.

### 3.3.2 Identification of the World Genera of the Gyrophaenina

#### 3.3.2.1 Notes about the Key and its Use

This key is intended for identification of the known genera of the Gyrophaenina of the world.
Relative positions of genera within the key imply nothing about relationships. Any similarity of various aspects of the key to lineages in the cladogram is an incidental result of relative usefulness of phylogentically important characters as "key" characters.

Lohse (1974) pointed out that mouthparts are most useful for delimiting higher taxa among aleocharines. However, because of difficulty of observing mouthpart structure, his key is based on other characters. I prefer to use easily seen characters as important key characters, but the most reliable characters for arranging the genera of gyrophaenines in groups are those of the mouthparts, particularly structure of the ligula. Though Seevers (1978) states that structure of the ligula is not as reliable for classification of aleocharines as has been implied by its use in the past, such characters appear quite stable within genera or supergeneric taxa among gyrophaenines. Therefore, I have used form of this structure near the beginning of the key. Ligulae are very difficult to observe in many gyrophaenines, especially very small specimens. However, once observed, the structure provides unambiguous entrance into the proper part of the key. Other characters provided aid in identification of gyrophaenines when ligula structure cannot be observed. However, states of these characters are more variable and qualitative, and more subject to interpretation, and must be used with caution.

To my knowledge, structure and form of the setal patch on tergum 10 have not been previously used to identify aleocharines. Among gyrophaenines this is very useful, though it is difficult to observe if the abdomen is contracted. Because of overlap in external structure, specimens of a few gyrophaenine genera are most reliably identified by aedeagal or spermathecal features. I have used aedeagal structure as a major key character for separation of *Probrachida* and *Brachida*, and as a secondary character for identification of *Agaricomorpha*. In all of these genera, form of the median lobe is quite distinctive.

In uncertain identifications, geographical range of a genus is useful. Therefore, known ranges of members of each genus are given in the key. Differences in useful key characters between specimens of Holarctic and New Zealand *Encephalus* make it most useful to key them out in separate couplets. This division also helps emphasize that these two groups presently placed in *Encephalus* may not belong to the same genus (see discussion in Section 3.3.3.4).

Reliable identification of genera of gyrophaenines, and indeed of most aleocharines, is difficult. This results primarily from small size of the beetles and subsequent difficulty in observing reliable key characters. Confident identification requires softening, clearing and dissection of many beetles, and observation under high magnification. Reluctance to use characters which require such specialized handling for identification is, at least in part, a cause of the present difficulty and uncertain reliability of most available keys. Aleocharines of such small size cannot be effectively handled using techniques appropriate to larger beetles.

### 3.3.2.2 Key for the Identification of the Known Genera of the Subtribe Gyrophaenina of the World

1 (0) Ligula broadly rounded (Figure 103, 105-109). Pronotum hind margins not or slightly bisinuate. Elytral apico-lateral angles not or, at most, slightly sinuate ..................................2

1' Ligula more or less protruded and parallel-sided, entire (Figure 98) or bifid (Figure 111). Pronotum hind margins markedly, slightly, or not bisinuate. Elytral apico-lateral angles markedly, slightly, or not sinuate ......................................4

2 (1) Body markedly robust, broadly oval in dorsal aspect. Microsetae sparse, body subglabrous. Head deflexed and in more or less vertical plane, base covered by anterior margin of pronotum. Mesosternum in more or less vertical plane. Holarctic region .......... *Encephalus* Kirby (part)

2' Body moderately to slightly robust, elongate-oval to more or less parallel-sided in dorsal aspect. Microsetae very to moderately dense, body pubescent. Head slightly or not deflexed, base slightly or not covered by anterior margin of pronotum. Mesosternum not in vertical plane .....3

3 (2') Labium with 2 medial setae. Without pair of macrosetae on vertex of head. Aedeagus distinctive; apical process of median lobe not highly modified; flagellum exerted, long, whip-like, not coiled inside basal capsule (Figures 202, 203). New World tropics ........................................ *Probrachida* new genus

3' Labium with 1 medial seta. With pair of macrosetae on vertex of head (Figure 15). Aedeagus distinctive; apical process of median lobe modified or not; flagellum not exerted, coiled inside basal capsule (Figures 204-206). Old World ..................................... *Brachida* Mulsant and Rey

4 (1') Ligula bifid in at least apical 1/3. Hypomera not (in most) or slightly visible in lateral aspect. Mesosternum carinate or not ......................5

4' Ligula entire, more or less protruded and parallel sided (Figure 98) or slightly tapered to apex (Figure 100). Hypomera not, slightly or entirely visible in lateral aspect. Mesosternum carinate in apical 2/3 or not carinate (in most) ...........11

5 (4) Body subglabrous. Lateral macrosetae on prothorax, elytra and abdomen extremely prominant, large, dark and bristle-like (Figure 231). Southeast Asia .... ................................ *Adelarthra* Cameron

5' Body markedly to moderately pubescent. Lateral macrosetae of prothorax, elytra and abdomen not extremely prominent, or, if enlarged, not markedly so and limited to prothorax and/or elytra ........6

6 (5') Ligula as long as labial palpomere 1, bifid in apical 1/3 (Figure 115). Southeast Asia .......... ................................ *Neobrachida* Cameron

6' Ligula shorter than labial palpomere 1, bifid at least 1/2 distance to base .......................7

7 (6') Setal patch on tergum 10 more or less square, not incised posteriorly to form a chevron-shaped patch ..................................................8

7' Setal patch on tergum 10 incised posteriorly to form a chevron-shaped patch, or patch of 1 to 3 distinct rows of setae ...........................9

8 (7) Mesosternal and metasternal processes fused, suture indistinguishable. Southeast Asia, India .......................................... *Pseudoligota* Cameron

8' Mesosternal and metasternal processes not fused, suture distinct. Palearctic region ............................................ *Agaricochara* Kraatz

9 (7') Setal patch on tergum 10 chevron-shaped (Figure 175) but setae not in 1 to 3 distinct rows. Aedeagus distinctive, apical lobe laterally displaced from flagellum insertion (Figures 214, 215). Nearctic, Neotropical regions ........................................ *Agaricomorpha* new genus

9' Setal patch on tergum 10 in 1 to 3 distinct chevron-shaped rows (Figures 170, 171, 174). Aedeagus not as above ..........................10

10 (9') Body form very robust, broadly oval in cross section. Mesosternum either not carinate or with low diffuse ridge medially. Head moderately deflexed into vertical plane. Mexico, Central America, West Indies ............. *Brachycara* Sharp

10' Body form not robust, more or less flattened in cross section. Head not or slightly deflexed into vertical plane. Southeast Asia, India ............ .............................. *Sternotropa* Cameron

11 (4') Mesosternum carinate in at least anterior 2/3. Body very robust, broadly oval in dorsal aspect. Elytral apico-lateral angle markedly sinuate. New Zealand ................... *Encephalus* Kirby (part)

11' Mesosternum not carinate. Body moderately robust to not robust, elongate oval to parallel-sided in dorsal aspect. Elytral apico-lateral angle moderately to not sinuate .......................12

12 (11') Setal patch on tergum 10 in distinct V-shaped row (Figure 166). Prothorax markedly transverse, 2.0 times as wide as long or wider. Body of most specimens moderately to very pubescent. Antennae of most specimens short, with antennomeres 4 to 10 markedly transverse, in form of loose parallel-sided club (Figure 26). New World ................ .................................. *Eumicrota* Casey

12' Setal patch on tergum 10 more or less square (Figures 162-164). Prothorax of most specimens 1.2 to 1.7 times as wide as long. Body of most specimens slightly pubescent to subglabrous. Antenna short or elongate, with antennomeres 4 to 10 slightly transverse to elongate or various in same specimen ...................................13

13 (12') Eyes extremely large, occupying most of lateral margins of head (Figure 12, 13). World Wide ...... .................................. *Phanerota* Casey

13' Eyes moderate in size (Figure 7-11). World Wide .. ............................ *Gyrophaena* Mannerheim

### 3.3.3 Genera of the Gyrophaenina

#### 3.3.3.1 Genus *Gyrophaena* Mannerheim

(Figures 7-11,21-24, 29-32, 56, 73, 74, 98, 99, 119-122, 131, 137, 142, 143, 149, 156, 162, 163, 176-178, 192-194, 216, 218, 233, 234, 240, 241, 245, 246)

*Gyrophaena* Mannerheim 1830:488. Type species: *Gyrophaena nana* (Paykull) (from *Staphylinus*). Fixed by Westwood 1838:20 by subsequent designation.

Mannerheim 1830:488. Erichson 1837:365. Erichson 1839-40:182. Lacordaire 1854:43. Kraatz 1856-58:352. Jacque du Val 1857-59:18. Thomson 1860:266. Mulsant and Rey 1871:17. Fauvel 1872:297. Fowler 1888:183. Gangelbauer 1895:297. Casey 1906:278. Reitter 1909:83. Blatchley 1910:340. Fenyes 1918:95. Cameron 1920:354, 359. Cameron 1922:368. Bernhauer 1926:323. Scheerpeltz 1930:70. Wusthoff 1937:137. Cameron 1939:56. Scheerpeltz and Höfler 1948:163. Seevers 1951:673. Likovsky 1964:52. Batten 1973:63. Lohse 1974:21. Seevers 1978:161.

*Diagnostic combination*. – Ligula entire, produced as more or less parallel-sided lobe. Eyes moderate in size. Hypomera slightly to broadly visible in lateral aspect. Mesosternum without medial longitudinal carina. Setal patch on tergum 10 more or less square, setae flattened. In addition, most members of *Gyrophaena* are distinguished by the subglabrous body; broadly oval or subquadrate pronotum (1.3 to 1.6 times as wide as long); more or less transverse head (1.1 to 1.3 times as wide as long); and prosternum with slight transverse carina and without medial knob, carina or protuberance.

*Description*. – Length 1.0 to 3.0 mm. Body parallel-sided, slightly flattened (in most specimens) to slightly robust. Sculpture reticulate, obsoletely reticulate or smooth, but uniform throughout or various on different regions of body. Surface subshining to shining in most species, dull in some; moderately to slightly pubescent, subglabrous, or glabrous, individuals of most species slightly pubescent to subglabrous.

*Head*. (Figures 7-11) – More or less transverse in most species, subquadrate to elongate in some; head held more or less in plane of body. Sculpture various. Microsetae numerous, short and stiff, to fewer, longer and more widely scattered. Punctures small to large, asperite in specimens of some species. Pair of darker macrosetae medially on vertex of head in specimens of a very few species (Figure 10), absent from most. Eyes moderate in size. Infraorbital carina moderately to markedly developed. Neck carina well developed. Antennae very variable within genus. Antennomere 4 similar to 1-3.

*Mouthparts*. – Labrum (Figures 29-32) with major setae distinct, additional setae absent. Sensilla of medial sensory area well distinct. Lateral sensilla row distant from lateral margin. Maxilla (Figures 73, 74, 233, 234) with tip of lacinia truncate with well developed "spore brush". Number and size of teeth various; relatively few, large, widely spaced teeth (Figure 233) to moderately numerous, smaller, more closely spaced teeth. Internal face of lacinia with single row of many to few, large setae, and 3 or 4 widely spaced hyaline sensilla. Galea with apical setae in 4 distinct rows, setae subspatulate to plate-like. Mandibles (Figure 56) not bifid at tip. Right mandible with small to large internal tooth. Prostheca typical of subtribe. Labium (Figures 98, 99) with ligula undivided, entire, produced as a more or less parallel-sided lobe. Medial seta 1 or, in specimens of a few species, absent.

*Thorax* – Prothorax transverse, broadly oval to subquadrate; specimens of most species with slightly transverse, broadly oval pronota, 1.6 to 1.3 times as wide as long (Figures 119-122); flat, slightly convex or moderately convex in cross section, sides not, slightly, or, in some species, moderately depressed; antero-lateral borders not markedly depressed. hypomera not, partially, or fully visible in lateral aspect; anterior margin straight or broadly rounded; Posterior margin slightly to, in most specimens, not at all bisinuate, hind margin of some species with a slight to moderate medial emargination. Sculpture reticulate, obsoletely reticulate, or smooth, integument subshining to markedly shining. Microsetae various: numerous, more or less densely and uniformly distributed (surface pubescent), to very few and widely scattered (surface subglabrous to glabrous); punctures small to large, asperite or not. Macrosetae small and inconspicuous to large and conspicuous; arrangement typical of subtribe. Punctures of macrosetae in medial row of many large, conspicuous. Elytra shorter than, equal to or longer than pronotum. Outer apical angles slightly to not at all sinuate (Figure 131). Integument reticulate to smooth, subshining to markedly shining. Microsetae numerous to few, uniformly distributed, punctures small to large, asperite in many species. Macrosetae inconspicuous to conspicuous. Prosternum transverse to slightly transverse. Specimens of most species with slight transverse raised ridge or carina (Figure 142, 143), or transverse carina absent. Without prominant medial knob, carina or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process varied in length, extended from slightly beyond middle of mesocoxal cavities to posterior margin of coxal cavities. Metasternal process truncate or broadly rounded. Isthmus absent. Suture between meso- and metasternal process fused in some species, distinct in most. Coxae widely separated. Setae on metepisternum numerous to few, in single row, setose area more or less delimited ventrally by fine carina or not (Figures 156, 245, 246). Tarsomere 1 of hind legs various: equal in length to second tarsomere to as long as next two combined (slightly longer in a few species); tarsomere 1 of hind leg with a slightly to markedly developed ctenidium on inner ventral surface.

*Abdomen*. – Flattened to slightly robust; sides parallel. Terga 3-5, 3-6 or 3-7 markedly to slightly transversely impressed. Sterna 3-5 very slightly transverely impressed to unmodified. Tergum 7 with anterior border modified as openings for abdominal gland ducts. Tergum 10 with setal patch more or less square; setae numerous to few, flattened, subspatulate to spatulate.

*Aedeagus*. (Figures 192-194) – Extremely varied among species. Median lobe with apical process simple to strongly modified and complex, asymmetrical in many; flagellum tubular, whip-like or very complex. Parameres (Figures 216, 217) simple to complex and asymmetrical.

*Spermatheca*. – Typical of subtribe; simple (Figures 176, 178) or with slightly elongate neck (Figure 177).

*Secondary sexual characteristics*. – Very varied. Males of most species with posterior margin of tergum 8 broadly or narrowly incised, incision with more or less well developed spines on each side, with or without 1 or more teeth or spines medially within incision. Many males with tergum 7 with carinae, spines or knobs. Other terga modified or not. Some males with spines, carinae or aperities on elytra. Males of some with sternum 8 emarginate medially. Some males with tergum 10, fewer with tergum 9 or sternum 10, modified. Females of some species with integumental modifications; if so, males and females of same species with markedly to slightly different modifications.

*Discussion*. - *Gyrophaena* as presently recognized is the most heterogenous genus among gyrophaenines. Typically, members have been recognized by presence of widely separated coxae, exposed hypomera and moderately sized eyes (Seevers 1951), or these in addition to a transverse head and shining subglabrous integument (Lohse 1974). This combination is inadequate for recognition of all species that should be placed in this genus, resulting in confusion about limits of the genus as indicated by, among other things, the question of whether or not *Agaricochara* Kraatz should be considered a subgenus of *Gyrophaena*. The characters provided in the diagnostic combination should help clarify assignments to this genus.

No derived character state is shared among all members of *Gyrophaena*. Therefore, as presently conceived, *Gyrophaena* cannot be shown to represent a monophyletic assemblage. It is, instead, paraphyletic in relation to *Phanerota* (see Section 4.2.2.8.2). This appears to result from the great heterogeneity of forms now included within *Gyrophaena*. It seems likely that *Gyrophaena* could be divided into several genus-level monopyletic groups. This, however, would require detailed study of the world *Gyrophaena*, a monumental task.

Within *Gyrophaena*, a number of monophyletic groups are recognized. General form of the median lobe of the aedeagus and structure of secondary sexual modifications are most useful for recognition of monophyletic groups, but antennal structure, sculpture, pubescence and general body dimensions may be useful in combination with aedeagal structures. Seevers (1951) used primarily aedeagal structure in forming his "species groups", most of which were probably monophyletic.

*Natural history*. – Most members of *Gyrophaena* are found on fleshy gilled mushrooms as both larvae and adults. Some are more common on fleshy polypores (see Table 4). Donisthorpe (1935), Scheerpeltz and Höfler (1948) and Benick (1952) give host mushroom lists for European *Gyrophaena*. White (1977) has studied general characteristics of host mushrooms of members of *Gyrophaena*. Few details of life history and habits of individual species are available (see Section 3.1.2).

*Immature stages*. – Few detailed studies of immature stages are available. Larvae of *G. affinis* Sahlberg (Rey 1886), *G. cristophera* Cameron (Paulian 1941), *Gyrophaena* sp. (Böving and Craighead 1930), *G. gentilis* Erichson (White 1977) and *G. strictula* Erichson (White 1977) have been described. Of these, only White (1977) and Paulian (1941) provide detailed descriptions and illustrations. Larvae described as that of *G. manca* Erichson by Haeger (1853) are not *Gyrophaena* (see White 1977).

*Distribution*. – Members of the genus *Gyrophaena* occur throughout the world, except, as far as is known, in alpine and tundra areas.

*Major literature*. - Few papers about *Gyrophaena* include keys or illustrations, and descriptions are inadequate. The European fauna is best known. Keys and descriptions of European *Gyrophaena* are provided by a number of faunal studies including: Scheerpeltz and Höfler (1948) (areas around Vienna, Austria), Lohse (1974) (middle Europe), Seevers (1951) (with North American fauna), Wusthhöff (1937) (European fauna), Likovsky (1964) (Czechoslovakian fauna), and White (1977) (British fauna). Seevers (1951) provides keys, descriptions and illustrations of North American species. Cameron (1939) provides keys and descriptions of the known Indian species. No other comprehensive faunal studies of *Gyrophaena* with adequate keys and descriptions are available.

### 3.3.3.1.1 Review of the Subgenera of *Gyrophaena* Mannh.

#### 3.3.3.1.1.1 Historical Review

Genera and subgenera associated with the name *Gyrophaena* are a complex of inadequately defined and arbitrarily arranged groups, as indicated by the various treatments of them summarized here. Casey (1906, 1911) recognized four genera within his subtribe Gyrophaenae: *Phanerota* Csy., *Phaenogyra* Muls. and Rey, *Eumicrota* Csy. and *Gyrophaena* Mannh. Fenyes (1918) assigned subgeneric rank to *Phanerota*, *Phaenogyra* and *Eumicrota*. However, he recognized that *Phanerota* may warrant consideration as a genus. He retained the genus *Agaricochara* Kraatz for several species that occur in Europe and America, separating it from *Gyrophaena* by the bifid ligula, wider pronotum and less conspicuous eyes of the former.

Scheerpeltz and Höfler (1948) recognized three subgenera of European *Gyrophaena*: *Gyrophaena s.st.*, *Phaenogyra* and *Leptarthrophaena* Scheer. and Hof. Within *Phaenogyra* were placed those species in which the head of adults was relatively long in relation to interocular width. They established the subgenus *Leptarthrophaena* to include those species in which adults have antennomeres 5-10 distinctly elongate. In addition, they retained the genus *Agaricophaena* Reitter for *A. boleti* (L.).

Seevers (1951) eliminated the subgenus *Phaenogyra* and assigned the species to species group status, claiming that it was no more deserving of subgeneric status than most other species groups within *Gyrophaena s.st*. In addition, he showed that *Leptarthrophaena* was a conglomerate of several unrelated species, and that *Gyrophaena* could not be divided into subgenera solely on the basis of antennal structure of adults. Seevers followed Fenyes (1918) in recognizing *Eumicrota* Csy. as a subgenus, but reduced *Agaricochara* Kr. to subgeneric status within *Gyrophaena*. He separated adults of *Eumicrota* and *Agaricochara* on the basis of adult antennal character states (in spite of his previous statement that this was impossible). He believed that they are closely related and may be combined into a single genus when more is known about the Neotropical forms. He was unable to separate *Agaricophaena* and placed it in synonymy with *Agaricochara*. Finally, Seevers reassigned generic rank to *Phanerota* although he did not give reasons for doing so. He also recognized that the subgenus *Acanthophaena* Cameron was synonymous with *Phanerota*. Seevers (1978) raised *Eumicrota* and *Agaricochara* to generic rank.

At one time or another 11 subgenera (including *Gyrophaena s.st.*) have been assigned to *Gyrophaena* Mannh. In this revision three are given to generic rank: *Agaricochara* Kraatz, *Eumicrota* Casey and *Phanerota* Casey; *Acanthophaena* Cameron is placed as a subgenus of *Phanerota* and *Leptarthophaena* is shown to be indefinable (as pointed out by Seevers (1951)). Additionally, *Allocota* Bernhauer is not a member of the Gyrophaenina.

### 3.3.3.1.1.2 Key to the Described Subgenera

For reasons given above, this key does not include the following taxa: *Agaricochara* Kraatz, *Eumicrota* Casey, *Phanerota* Casey, *Leptarthrophaena* Scheerpeltz and Höfler, *Acanthophaena* Cameron, and *Allocota* Bernhauer. Taxa included are not necessarily monophyletic, nor is the key likely to assign members of all species to useful groups when the world fauna is considered.

1 (0) Abdomen of male with lateral margins of sterna 3 and 4 produced as spines or appendiculate processes ........................ *Enkentrophaena* Eichelbaum

1' Abdomen of male without lateral margins of sterna 3 and 4 produced as spines or processes ............2

2 (1') Head transverse (1.2 to 1.4 times as wide as long); moderately and obliquely narrowed behind the eyes. Specimens of most species slightly pubescent to subglabrous ....................................3

2' Head slightly transverse to longer than wide (1.1 to 0.8 times as wide as long); slightly and gradually narrowed behind the eyes. Specimens of most species moderately pubescent ................4

3 (2) Large (adults 3.0 to 3.5 mm in length); very robust. Terga 3 and, in some, 4, of males with median keel. Antennomere 4 longer than broad ..... .......................... *Orphnebioidea* Schubert

3' Smaller (adults 1.0 to 3.0 mm in length); less robust, most more or less flattened and parallel-sided. Terga 3 and 4 of males without median keel. Most with antennomere 4 quadrate or transverse ...................... *Gyrophaena s.st.*

4 (2') Larger (adults 1.3 to 2.1 mm in length). Head 1.2 to 0.7 times as wide as long. Pronotum 1.5 to 1.1 times as wide as long .................................................. *Phaenogyra* Muslant and Rey

4' Smaller (adults 0.9 to 1.2 mm in length). Head 1.2 times as wide as long. Pronotum 1.5 times as wide as long ...................... *Agaricophaena* Reitter

### 3.3.3.1.1.3 The Described Subgenera of *Gyrophaena* Mannh.

#### 3.3.3.1.1.3.1 Subgenus *Gyrophaena s.st.*

*Gyrophaena* Mannerheim 1830:488. Type species: *Gyrophaena nana* (Paykull).

Gangelbauer 1895:300. Fenyes 1918:97. Cameron 1939:65. Scheerpeltz and Höfler 1948:163. Seevers 1951:673. Lohse 1974:27.

#### 3.3.3.1.1.3.2 Subgenus *Agaricochara* Kraatz

*Agaricochara* Kraatz 1856:361. Type species: *Agaricochara laevicollis* Kraatz. Fixed by Kraatz 1856:361 by monotypy.

Kraatz 1856:361 (genus). Mulsant and Rey 1871:90 (genus). Gangelbauer 1895:304 (genus). Casey 1906:278 (genus). Reitter 1909:85 (genus). Fenyes 1918:92 (genus). Scheerpeltz 1930:70 (genus). Seevers 1951:740 (subgenus of *Gyrophaena*). Lohse 1974:130 (genus). White 1977:304 (subgenus of *Gyrophaena*). Seevers 1978:163 (genus).

*Notes*: Treated as a genus in this revision.

#### 3.3.3.1.1.3.3 Subgenus *Phaenogyra* Musant and Rey

*Phaenogyra* Mulsant and Rey 1872:166. Type species: *Phaenogyra strictula* (Erichson) (from *Gyrophaena*). Fixed by Fenyes 1918:24 by subsequent designation.

Mulsant and Rey 1871:76 (genus). Gangelbauer 1905:303 (genus). Casey 1906:278 (genus). Reitter 1909:85 (subgenus of *Gyrophaena*). Fenyes 1918:101 (subgenus of *Gyrophaena*).

Cameron 1939:140 (subgenus of *Gyrophaena*). Scheerpeltz and Höfler 1948:177 (genus). Seevers 1951:724 (*G. strictula* species group of *Gyrophaena*). White 1977:304 (within subgenus *Agaricochara*).

### 3.3.3.1.1.3.4 Subgenus *Eumicrota* Casey

*Eumicrota* Casey 1906:280. Type species: *Eumicrota corruscula* (Erichson) (from *Gyrophaena*). Fixed by Fenyes 1918:22 by subsequent designation.

Casey 1906:280 (genus). Fenyes 1918:101 (subgenus of *Gyrophaena*). Seevers 1951:732 (subgenus of *Gyrophaena*). Seevers 1978:162 (genus).

*Notes:* Treated as a genus in this revision.

### 3.3.3.1.1.3.5 Subgenus *Phanerota* Casey

*Phanerota* Casey 1906:285. Type species: *Phanerota fasciata* (Say) (from *Gyrophaena*). Fixed by Blackwelder 1952:299 by subsequent designation.

Casey 1906:285 (genus). Fenyes 1918:96 (subgenus of *Gyrophaena*). Seevers 1951:747 (genus). Seevers 1978:162 (genus).

### 3.3.3.1.1.3.6 Subgenus *Orphnebioidea* Schubert

*Orphnebioidea* Schubert 1908:611. Type species: *Orphnebioidea rosti* (Schubert) (from *Gyrophaena*). Fixed by Schubert 1908:611 by monotypy.

Schubert 1908:611 (subgenus). Fenyes 1918:97 (subgenus). Cameron 1939:61 (subgenus).

### 3.3.3.1.1.3.7 Subgenus *Agaricophaena* Reitter

*Agaricophaena* Reitter 1908:85. Type species: *Agaricophaena boleti* (Linaeus) (from *Staphylinus*). Fixed by Reitter 1909:85 by original designation.

Reitter 1909:85 (subgenus of *Gyrophaena*). Fenyes 1918:102 (subgenus of *Gyrophaena*). Scheerpeltz and Höfler 1948:163 (genus). Seevers 1951:740 (within subgenus *Agaricochara*). Likovsky 1964:53 (within subgenus *Agaricochara*). White 1977:311 (within subgenus *Agaricochara*).

### 3.3.3.1.1.3.8 Subgenus *Enkentrophaena* Eichelbaum

*Enkentrophaena* Eichelbaum 1913:139. Type species: *Enkentrophaena plicata* (Fauvel) (from *Gyrophaena*). Fixed by Blackwelder 1952:149 by subsequent designation.

Eichelbaum 1913:139 (subgenus of *Gyrophaena*). Fenyes 1918:96 (subgenus of *Gyrophaena*). Cameron 1939:57 (subgenus of *Gyrophaena*).

### 3.3.3.1.1.3.9 Subgenus *Acanthophaena* Cameron

*Acanthophaena* Cameron 1934:23. Type species: *Acanthophaena appendiculata* (Motschulsky) (from *Gyrophaena*). Fixed by Blackwelder 1952:34 by subsequent designation.

Cameron 1934:23 (subgenus of *Gyrophaena*). Cameron 1939:59 (subgenus of *Gyrophaena*).

*Notes:* Treated as a subgenus of *Phanerota* Casey in this revision.

### 3.3.3.1.1.3.10 Subgenus *Leparthrophaena* Scheerpeltz and Höfler

*Leptarthrophaena* Scheerpeltz and Höfler 1948:64. Type species: *Leptarthrophaena affinis* (Sahlberg) (from *Gyrophaena*). Fixed by Blackwelder 1952:215 by subsequent designation.

Scheerpeltz and Höfler 1948:64 (subgenus of *Gyrophaena*).

Seevers 1951:670-671 (shown to be untenable subgenus).

### 3.3.3.1.1.3.11 Subgenus *Allocota* Bernhauer

*Allocota* Bernhauer 1916:428. Type species: *Allocota abnormalis* Bernhauer. Fixed by Bernhauer 1916:428 by monotypy.

Bernhauer 1916:428 (subgenus of *Gyrophaena*).

*Notes:* According to Blackwelder (1952), *Allocota* Bernhauer is a junior homonym of *Allocota* Motschulsky 1860, Foerster 1868, and Meyrick 1904; and a synonym of *Razia* Bernhauer (renamed by Blackwelder 1952:82). Blackwelder (1952:46) transferred this taxon to *Bolitochara* Mannerheim as a subgenus.

### 3.3.3.2 *Phanerota* Casey

(Figures 12, 13, 25, 33, 34, 58, 75, 76, 100, 101, 123, 132, 144, 151, 161, 164, 165, 179, 180, 195, 196, 218)

*Phanerota* Casey 1906:285. Type species: *Phanerota fasciata* (Say) (from *Gyrophaena*). Fixed by Blackwelder 1952:299 by subsequent designation.

Casey 1906:285. Fenyes 1918:96. Cameron 1934:23. Cameron 1939:59. Seevers 1951:747. Seevers 1978:162

*Diagnostic combination*. — Eyes extremely large, extended almost entire length of lateral margins of head. Ligula entire, protruded, more or less parallel-sided. Microsetae sparse, integument subglabrous. Spermatheca with neck elongate and coiled proximal to plate-like flange. Aedeagus form distinctive (Figures 195, 196).

*Description*. — Length approximately 1.5 to 3.0 mm. Body more or less flattened, parallel-sided. Sculpture reticulate, obsoletely reticulate, or smooth, uniform throughout body or various on different sclerites, surface subshining to markedly shining. Body slightly pubescent to subglabrous; microsetae few, small and scattered in specimens of most species; punctures moderate to small, asperite or not. Macrosetae moderately large and conspicuous or rather small and inconspicuous.

*Head*. (Figures 13, 14) — More or less transverse, held more or less in plane of body. Sculpture various. Microsetae various, specimens of most species with few to very few widely scattered microsetae; punctures moderate to very fine. Macrosetae two pairs, one medial to each of anterior and posterior margins of eye, or absent. Eyes very large, globose, extended most of length of lateral margin of head, tempora obsolete; eyes coarsely faceted. Infraorbital carina markedly to very markedly developed, complete ventrally as medio-ventral margin of eyes, or obsolete anteriorly. Neck carina markedly developed. Antenna various, typical of subtribe. Antennomere 4 similar to 1-3. Antennomere 4 subquadrate to elongate; 5-10 elongate, subquadrate or slightly transverse (Figure 25).

*Mouthparts*. - Labrum (Figures 33, 34) with major setae distinct, additional setae absent. Sensilla of medial sensory area well developed. Lateral sensilla row distant from lateral margin. Maxilla (Figure 75, 76) with tip of lacinia with well developed "spore brush". Teeth relatively large, close to moderately spaced. Internal face of lacinia with moderate to many large to medium sized setae and 2 or 3 widely spaced hyaline setiform sensilla. Galea with apical setae in 4 distinct rows, setae flattened, subspatulate to plate-like. Mandible (Figure 57, 58) rather robust, not bifid at tip. Right mandible with large internal tooth. Prostheca typical of subtribe. Labium (Figure 100, 101) with ligula entire, produced as a more or less parallel-sided lobe, sides slightly convergent from base to more or less broad apex in specimens of some species; apical half of ligula inclined ventrally in specimens of some species. Medial seta 1 reduced or absent in specimens of many species.

*Thorax.* (Figure 123) – Pronotum slightly transverse, broadly oval in outline, approximately 1.3-1.6 times as wide as long. Flat or slightly convex in cross section, sides not or slightly depressed; antero-lateral border not markedly depressed. Hypomera partially to fully visible in lateral view. Anterior margin straight or broadly rounded. Hind margin not bisinuate, not medially emarginate. Pronotal sculpture reticulate, obsoletely reticulate or smooth, integument subshining to markedly shining. Macrosetae small, few to very few, widely scattered, punctures fine to moderate. Macrosetae moderately large, conspicuous to small, inconspicuous; arrangement typical of subtribe. Elytra (Figure 132) equal to or slightly longer than pronotal length; outer apical angles very slightly to not at all sinuate; sculpture reticulate to smooth; microsetae few, widely scattered; punctures medium to fine, asperite or not; macrosetae moderately large to small. Prosternum (Figure 144) transverse to slightly transverse; with or without fine transverse carina, or carina obsolete medially; without medial spine, carina or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process extended to middle or slightly posterior to middle of midcoxal cavities (Figure 151). Metasternal process extended anteriorly in broad contact with mesosternal process, suture unmodified, not fused. Isthmus absent. Apex of metasternal process truncate or broadly rounded.

Coxae widely separated. Metepisternal setae numerous to few, in single row; setose area delimited antero-laterally by fine carina or not. Hind tarsus (Figure 161) with first tarsomere as long as next 2 together, or, in specimens of some species, 1.0 to 1.5 times length of tarsomere 2: with well developed ctenidium on ventral surface.

*Abdomen*. – More or less flattened. Sides parallel. Terga 3-5 or 3-6 markedly to moderately transversely impressed. Sterna unmodified. Tergum 7 with anterior border modified as opening for abdominal gland ducts. Tergum 10 (Figures 164, 165) with medial setal patch more or less square, setae numerous to few, flattened, subspatulate.

*Aedeagus*. – (Figures 195, 196, 218) Known species with apical lobe of median lobe long, slender, and spine-like. Flagellum long, slender, more or less whip-like. Parameres not exceptionally modified (Figure 218).

*Spermatheca*. – Neck elongate, coiled and/or convoluted proximal to plate-like flange (Figures 179, 180).

*Secondary sexual characteristics*. – Both males and females with tergum 8 shallowly to deeply emarginate medially. Females with middle of emargination unmodified or with very broad low lobe internally. Males with emargination with more or less distinct lobe internally. Males of some species with carina near postero-lateral margin of elytra. Males of some species with lateral margins of sternite 5 modified as leaf-like lobe and/or lateral paratergite 5 with thick spine. Males of some species may also have some tergites or paratergites broadened and flattened and/or transverse impressions of tergites deepened.

*Discussion*. – Casey (1906) described *Phanerota* to include several North American, West Indian and Mexican species. Fenyes (1918) ranked *Phanerota* as a subgenus of *Gyrophaena*, although he recognized that *Phanerota* may warrant generic status because he believed that the very large eyes crowd out the infraorbital carina. Seevers (1951) recognized *Phanerota* as a genus based primarily on the large eyes, lack of an infraorbital carina, and distinctive spermatheca. Both Seevers and Fenyes were incorrect since the infraorbital carinae are indeed present, although the large eyes encroach upon them so that the carinae form the medio-ventral margins of the orbit.

Seevers (1951) recognized that *Acanthophaena* Cameron was a *Phanerota*, but he did not formally place them in synonymy. Based on the shared characteristics of extremely large eyes, similar secondary sexual characteristics, particularly those on tergum 8, similar spermatheca, and similar median lobe of the aedeagus, it seems appropriate to consider *Phanerota* Casey and *Acanthophaena* Cameron to represent a single genus.

Therefore, two subgenera are recognized within*Phanerota* Casey, distinguished from each other mainly by secondary sexual characteristics of males. Additional study may show that characteristics on which these 2 subgenera are based are inadequate to define subgenera. Also, *Phanerota s.st.* may be paraphyletic with respect of *Acanthophaena*. However, since 2 distinct groups can be recognized at present, it seems most useful to retain two subgenera within this genus.

*Natural history*. – As far as is known, both adults and larvae occur between gills of fleshy mushrooms. Ashe (1981a) described the life history and habits of *Phanerota fasciata* (Say), and (in press) has discussed host relationships of *P. fasciata* and *P. dissimilis* (Erichson).

*Immature stages*. – Ashe (1981a) described larval instars and pupa of *Phanerota fasciata* (Say).

*Distribution*. – The majority of species of *Phanerota* are tropical or subtropical. A few species occur in temperate regions of North America and Asia. Species of *Phanerota s.st.* are known from eastern North America, West Indies, Mexico, Central America and South America. Species of *Acanthophaena* occur in Africa, India, Southeast Asia, Australia, New Guinea and Japan.

*Major literature*. – Adequate keys and descriptions are available only for the North American species (Casey 1906, Seevers 1951) and the Indian species (Cameron 1939).

### 3.3.3.2.1 Review of described Subgenera of *Phanerota* Casey

#### 3.3.3.2.1.1 Key to Described Subgenera

1 Males with sternum 5 with each lateral margin with large posteriorly directed lamelliform process. Males with terga and paraterga 3-5 or 3-6 very markedly broadened and flattened, and with transverse impressions deepened. Head with 2 macrosetae on each side of dorsum, one each medial to anterior and posterior margin of eye .......... .................................. *Acanthophaena* Cameron

1' Males without sternum 5 lateral margins with lamelliform process. Males with terga and paraterga 3-5 or 3-6 at most slightly broadened and flattened, and transverse impressions at most only slighty deepened. Head without macrosetae ............................ *Phanerota s.st.*

### 3.3.3.2.1.2 Subgenus *Phanerota* Casey *s.st.*

*Phanerota* Casey 1906:285. Type species: *Phanerota fasciata* (Say). Fixed by Blackwelder 1952:299 by subsequent designation.

*Diagnostic combination*. – Head with moderate to small more or less widely separated microsetae. Macrosetae absent. Males with tergum 8 broadly emarginate, lateral edges of emargination more or less extended as blunt tooth; medial area of emargination with broad lobe, slightly bifid at apex or not. Males of some species with acute carina on each elytron near apico-lateral margin; with or without elevation near each inner margin. At least some sterna of males thickened laterally or not, but not with marked lamelliform process. Some terga and paraterga of males broadened and flattened or not, and transverse impression deepened or not, but not to the extremes found among males of *Acanthophaena*.

### 3.3.3.2.1.3 Subgenus *Acanthophaena* Cameron

*Acanthophaena* Cameron 1934:23. Type species: *Acanthophaena appendiculata* (Motschulsky) (from *Gyrophaena*). Fixed by Blackwelder 1952:34 by subsequent designation.

*Diagnostic combination*. – Head with microsetae small, widely scattered. Macrosetae 2 on each side of dorsum, on each medial to anterior and posterior margin of eye. Males with tergum 8 similar to that of *Phanerota s.st.* Tergum 7 with or without carinae near apico-lateral margins. Sterna with or without some lateral margins thickened; sternum 5 with each lateral margin with well developed, posteriorly directed lamelliform process; lateral paratergum 5 broadened and with large posteriorly directed spine or not. Terga and paraterga 3-5 or 3-6 markedly broadened, flattened, and transverse impressions deepened.

### 3.3.3.3 *Eumicrota* Casey

(Figures 14, 26, 35, 59, 77, 102, 124, 125, 133, 139, 145, 166, 181, 197, 198, 219, 235, 247)

*Eumicrota* Casey 1906:280. Type species: *Eumicrota corruscula* (Erichson) (from *Gyrophaena*). Fixed by Fenyes 1918:22 by subsequent designation.

Casey 1906:280. Fenyes 1918:101. Seevers 1951:732. Seevers 1978:162.

*Diagnostic combination*. – Size small (most adults 1.0 mm or less in length). Pronotum transverse, 1.7-2.1 times as wide as long. Ligula entire, protruded, more or less parallel-sided. Tergum 10 with setal patch in distinct V-shaped row. Aedeagus form distinctive (Figure 197).

*Description*. – Minute to very small, length approximately 0.6 to 1.5 mm, adults of most species 1.0 mm or less in total length. Body of most dark, piceous, brownish-black or black. Body parallel-sided, flattened to slightly robust. Body sculpture reticulate throughout in most; integument shining to subshining; moderately to more or less strongly pubescent, setae short, numerous and uniformly and closely spaced in most species, setae fewer and less densely arranged in some. Punctures moderate to small, asperite in many.

*Head*. (Figure 14) – More or less transverse; held more or less in plane of body to slighly deflexed; sculpture reticulate. Microsetae short, numerous and densely arranged in most or fewer and more sparsely arranged. Punctures fine to minute. Macrosetae absent in specimens of most species, some with very small, difficult to distinguish, pair of macrosetae medially on vertex. Eyes moderate in size. Infraorbital carina complete, moderately to markedly developed. Neck carina distinct. Antenna (Figure 26) short, in majority of species not longer than head and pronotum together. Antennomere 4 similar to 1-3. Specimens of most species with antennomere 4 small, transverse to subquadrate; 5 wider than 4; 6-10 markedly transverse, subequal to 5 in width so that antennomeres 5-10 form a loose, parallel-sided club. Specimens of some species with antenna more elongate, article 4 longer than wide, 5 quadrate, and 6-10 transverse (see discussion below).

*Mouthparts*. – Labrum (Figure 35) with major setae distinct, additional setae absent. Medial sensory area with sensilla well developed; lateral sensory row present, distant from lateral margin, 3-4 sensilla. Mandibles

(Figure 59) typical of subtribe. Not bifid at apex. Right mandible with small tooth internally, or tooth very slightly developed. Maxilla (Figure 77, 235) with apex of lacinia truncate, with well developed "spore brush"; teeth of spore brush small, numerous and densely arranged in most. Internal face of lacinia with 3 or 4 large, hyaline setiform sensilla. Galea with apical setae in 4 distinct rows, setae subspatulate to plate-like. Labium (Figure 102) with ligula entire, produced as a more or less parallel-sided lobe; medial seta 1.

*Thorax*. – Pronotum (Figures 124, 125) markedly transverse, 1.7 to 2.1 times as wide as long; slightly to moderately convex in cross section, sides slightly to moderately depressed, antero-lateral borders moderately depressed. Hypomera narrowly visible to not visible in lateral view. Anterior margin of pronotum straight. Posterior margin moderately, very slightly, or in specimens of a few species, not at all bisinuate; posterior margin not emarginate medially. Pronotal sculpture reticulate; integument subshining or dull. Microsetae various, short, numerous, and uniformly distributed in most species to fewer and sparsely distributed; punctures sparse and fine to slightly asperite; macrosetae small, inconspicuous, difficult to distinguish from microsetae in most. Elytra (Figure 133) equal to or longer than pronotal length; outer apical angles moderately to very slightly sinuate; integument reticulate, subshining to dull; microsetae numerous, uniformly distributed in most species, asperitely punctate or not.; macrosetae inconspicuous, as in *Gyrophaena*. Prosternum (Figure 145) transverse to strongly transverse; with or without faint transverse carina; without prominent medial knob, carina or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process length various, extended from slightly beyond middle to posterior 1/4 of middle coxal cavities; juncture with metasternal process broadly truncate, suture fused in specimens of a few species. Isthmus absent. Coxae widely separated. Setae on metepisternum numerous to few, in single row; setose area not delimited by a carina or with very slight carina anteriorly. Tarsomere 1 of hind tarsus equal in length or slightly longer than 2, with indistinct ctenidium on inner surface.

*Abdomen*. – Flattened, sides parallel. Terga 3-5 (6 very slightly in some) moderately to slightly transversely impressed. Sterna unmodified. Tergum 7 with anterior border modified for opening of abdominal gland ducts. Tergum 10 (Figure 166) with medial setal patch arranged in distinct V-shaped rows; setae unmodified or flattened.

*Aedeagus*. (Figures 197, 198, 219) – Most species in genus with variation on very distinctive basic form. Median lobe with apical process slender and elongate; in most with knob or hook-like structure apically. Flagellum elongate, whip-like, and apical half or more tightly coiled. Parameres not extensively modified (Figure 219).

*Spermatheca.* (Figure 181) – Typical of subtribe, simple.

*Secondary sexual characteristics.* – Varied among species. Posterior margin of tergum 8 of male (and in some species, female) of many species broadly emarginate. Males of others with posterior margin of tergum 8 lobed or toothed medially. Other terga modified or not. Males of some species with lateral margin of sterna modified. Some tropical species with male and female with distinctively different sexual modifications.

*Discussion.* – Seevers (1951, 1978) believed that *Eumicrota* Casey was closely related to *Agaricochara* Kraatz, and the two genera should possibly be combined. He based this primarily on similarities in the very transverse pronotum and similar intercoxal processes. It appears, however, that *Eumicrota* and *Agaricochara* are not closely related within the Gyrophaenina (see Section 4.2.2.7.1). *Eumicrota* is a very distinct group, and, based on the derived characters of general form of the median lobe of the aedeagus and the V-shaped setal patch on tergum 10, it is almost certainly monophyletic.

Most members of *Eumicrota* have a characteristic habitus of small size, dark color, transverse pronota, and very transverse antennomeres. However, a few Neotropical gyrophaenines share the derived character states of *Eumicrota* (aedeagal form, and form of setal patch on tergum 10), but are larger and have a general habitus more similar to that of members of *Gyrophaena* s.st., and elongate antennomeres. *Gyrophaena varians* Sharp also has male and female specimens with markedly different secondary sexual characteristics. Because they share derived characters with other *Eumicrota*, these are here considered to belong to this genus.

*Natural history*. – As far as is known, members of *Eumicrota* are found most commonly on fleshy polypore mushrooms on logs. They can also be found in large numbers on some more persistent gilled mushrooms on logs, and on woody and/or resupinate polypore mushrooms (Seevers 1951, and personal observations).

*Immature stages*. – Immature stages of members of *Eumicrota* have not been described.

*Distribution*. – As far as is presently known, members of *Eumicrota* are limited to the New World. Most species are tropical or subtropical. Seven species occur in America north of Mexico. Two of these are widespread in eastern North America. Others are limited to the Gulf States or Southwest. Several described West Indian and Central American species should be assigned to this genus, and I have seen many undescribed species from Mexico, Central America and South America.

*Major literature*. – Only Casey (1906) and Seevers (1951) provide more or less useful keys and descriptions of members of *Eumicrota*. Both of these are North American in scope.

### 3.3.3.4 *Encephalus* Kirby

(Figures 36, 60, 61, 78-80, 103, 104, 134, 157, 167, 182, 183, 199, 200, 201, 220, 221)

*Encephalus* Kirby 1832:163. Type species: *Encephalus complicans* Kirby (in Stephens 1832:163). Fixed by Stephens 1832:163 by monotypy.

Kirby 1832:163. Kraatz 1856:351. Thomson 1860:265. Mulsant and Rey 1871:11. Fauvel 1872:360. Fowler 1888:151. Gangelbauer 1895:304. Casey 1906:85. Reitter 1909:85. Fenyes 1918:94. Scheerpeltz 1930:70. Seevers 1951:752. Lohse 1974:26. Seevers 1978:163.

*Diagnostic combination*. – (Holarctic species only) Very robust, broadly oval in dorsal aspect. Head markedly deflexed into vertical plane. Antenna short, as long as head and pronotum together; antennomeres 5-10 transverse, 6-10 forming a losse incrassate club. Pronotum markedly convex, hypomera not visible in lateral aspect. Ligula broadly rounded. Mesothorax in vertical plane. Mesosternal process very wide and long, extended to posterior margin of middle coxal cavities. Middle coxae very widely separated.

*Description*. – Length approximately 1.5 to 2.2 mm. Body shape broadly oval, robust, oval in cross section. Body sculpture markedly reticulate to reticulate throughout; body subshining. Body subglabrous, setae few, short, widely scattered; punctures small.

Head. – Slightly transverse, much narrower than anterior margin of prothorax; inclined, oblique to almost vertical; reticulate throughout; microsetae small, few, widely scattered; punctures very small to moderate; macrosetae absent. Eyes moderate in size. Infraorbital carina complete, well developed. Neck carina well developed. Antenna short, about as long as head and pronotum together. Antennomere 4 similar to 1-3. Antennomeres 5-10 transverse; 6-10 gradually increased in width distally, in form of loose incrassate club.

*Mouthparts.* – Labrum (Figure 36) with major setae distinct, without accessory setae; lateral sensilla row slightly developed or absent; medial sensory area with sensilla well developed or reduced. Mandibles (Figure 60) not bifid at apex, right mandible with small internal tooth. Prostheca typical of subtribe. Maxilla (Figure 78, 79) with tip of lacinia truncate with well developed spore brush; spines relatively thick and long, widely spaced. Setae on inner face of lacinia in single row. Inner face of lacinia with 3 or 4 widely spaced hyaline sensilla. Galea with apical setae in 4 distinct rows, setae subspatulate to plate-like. Labium (Figure 103) with ligula entire, produced as broadly rounded lobe. Medial seta 1.

*Thorax.* – Pronotum moderately to markedly transverse, 1.7 to 2.0 times as wide as long, markedly convex. Sides moderately depressed, in dorsal aspect narrowed and broadly rounded proximal to apical angles, these acute, very markedly depressed, embracing sides of head; hypomera not visible in lateral aspect; anterior margin straight or broadly emarginate and bisinuate, covering base of head; hind margin broadly rounded, not bisinuate, with medial emargination; sculpture reticulate throughout; microsetae few, slight, scattered, punctures small; macrosetae small, M.L.2 and M.L.4 very reduced, small or absent; punctures small. Each elytron wider than long; sutural length less than or subequal to pronotal length. Outer apical angles rounded, not sinuate; apical and sutural margin depressed and narrowly beaded; surface uniformly reticulate throughout; microsetae few to moderate in number, punctures very small to small. Prosternum slightly to moderately transverse with a slight transverse ridge; without prominent medial knob, carina or protuberance; markedly declivous posteriorly. Mesosternum markedly declivous with slight medial longitudinal carina, indistinct before apex of process or not carinate but with very slight, low, medial ridge in anterior 2/3. Mesosternal process very wide, extended to posterior margin of middle coxal cavities, apex truncate or broadly rounded. Metasternal process not extended between coxal cavities. Suture between processes complete, not fused, slightly raised into low bead. Metepisternum (Figure 157) with few setae in single row on posterior 1/3; setose area delimited by faint carina anteriorly. Tarsomere 1 of hind tarsus about as long as 2, with 6 to 7 setae in form of slight ventro-lateral ctenidium.

*Abdomen*. – Broadly oval in dorsal aspect, robust. Terga markedly transverse, together in form of broad flat plane. Terga 3-5 (or 3-6) slightly transversely impressed. Tergum 7 with anterior border modified for openings to abdominal gland ducts. Tergum 10 with setal patch more or less square; setae few to moderate in number, not flattened or subspatulate.

*Aedeagus*. (Figures 199, 200) – Median lobe with apical process simple, not highly modified. Flagellum slender, tubular. Parameres not markedly modified (Figures 220, 221)

*Spermatheca*. – Typical of subtribe, simple (Figure 182).

*Secondary sexual characters*. – Males of known species with posterior margin of tergum 8 with 4 slender spiniform processes.

*Discussion*. – Similarities in ligula structure, meso-metasternal processes, maxillary structure, general body form and aedeagal structure indicate that the Holarctic members of *Encephalus* form a monophyletic group. However, *Encephalus zealandicus* Fauvel and *E. latulus* Brown, while superficially similar in habitus to Holarctic species, differ from the description given above in a number of ways, including: smaller size (adults 1.1 to 1.3 mm in length); antennae longer, with club formed from antennomeres 5-10 less incrassate; lateral margins of pronotum not as markedly deflexed; pronotum hind margin not emarginate medially;' elytra very markedly sinuate on lateral apical angles; terga and paraterga not as markedly widened, abdomen not as robust; terga, paraterga and lateral margins of sterna with long, dark macrosetae; mesosternal process extended only 4/5 distance to posterior margin of middle coxae; labium with ligula very elonate, protruded, parallel-sided and entire (Figure 104); and different form of median lobe of aedeagus (Figure 201). Either the concept of *Encephalus* will have to be modified, or, as seems more likely, the New Zealand forms will have to be placed in a separate genus. Decision about which of these should be done requires a great deal more material than is available to me, and more comprehensive comparative studies within *Gyrophaena*, to which these forms are probably related. These studies are outside the scope of this treatment, and I only call attention to the problem here.

Relationships of *Encephalus* are unclear. The broad, undivided ligula is similar to that found in members of the "Brachida" lineage. However, in maxillary structure and many body characteristics, specimens of *Encephalus* are more similar to many members of *Gyrophaena*. The median lobe of the aedeagus of *E. americanus* Seevers and *E. complicans* Kirby is remarkably similar to that found in members of the *G. nana* species group of Seevers (1951).

*Natural history*. – Members of *Encephalus* are seldom found on fresh mushrooms. They are usually encountered in hay, rotting grass and hillocks in bogs (Lohse 1974).

*Immature stages*. – These have not been described.

*Distribution*. – Four species are known from the Palearctic region, 1 described species from the Nearctic region, and 2 described species from New Zealand (but see discussion above).

*Major literature*. – There is no comprehensive revision of the species of *Encephalus*. *E. americanus* Seevers is well described and illustrated by Seevers (1951) and *E. complicans* Kirby is well described and illustrated in a number of places in the European literature (*e.g.* Likovsky 1964, Lohse 1974).

### 3.3.3.5 *Probrachida* New Genus

(Figures 27, 37-41, 62-64, 91-84, 105-107, 168, 184, 202, 203, 222, 223, 224)

*Probrachida* new genus. Type species: *Probrachida modesta* (Sharp) (from *Brachida*). Fixed here by original designation.

*Diagnostic combination*. – Relatively large (adults 2.5 to 3.5 mm in length), more or less robust to parallel-sided. Head deflexed, oblique. Pronotum with apico-lateral margins deflexed, convex in cross section; hypomera not visible in lateral view; hind margin emarginate medially. Labium with ligula entire, broadly rounded; medial setae 2. Maxilla with setae on inner face of lacinia numerous, scattered, in most specimens; inner face of lacinia with additional teeth or spines (Figure 81-84). Galea with setae on apex in many very close rows; setae unmodified, filiform (Figure 83, 84). Aedeagal form distinctive (Figure 202, 203).

*Description*. – Length of adults 2.5 to 3.5 mm. Body robust, elongate, oval in dorsal aspect, or more or less parallel-sided. Sculpture reticulate to obsoletely reticulate, surface subshining to shining. Microsetae moderately short, densely arranged, body pubescent, or microsetae long, silky and very densely arranged, body subhirsute; punctures small, inconspicuous to large, distinct. Macrosetae small, inconspicuous to obsolete.

*Head*. – Slightly transverse, slightly or moderately deflexed to oblique plane; reticulate to obsoletely reticulate throughout; microsetae moderate in size to long and silky, densely arranged; macrosetae absent. Eyes moderate in size. Infraorbital carina complete, moderately to markedly developed. Neck carina well developed. Antenna as long as head, prothorax and 1/2 of elytra together. Antennomere 4 elongate, similar to 5-10 or similar to 1-3 (Figure 27), or intermediate in some; 5-10 elongate or 7-10 subquadrate. Antenna parallel-sided from antennomeres 3-10 or 4-10.

*Mouthparts*. – Labrum (Figures 37-41) with major setae distinct and moderately well developed, or difficult to distinguish from numerous accessory setae. Lateral sensilla row well developed, of 5 to 7 small, spine-like sensilla, at lateral margin. Medial sensory area with sensilla variously developed. Mandibles (Figures 62-64) both, left only, or neither bifid at apex; right with or without an internal tooth; prostheca typical of subtribe or with medio-internal area of fimbriate fringes of spine-like rather than bifid structures. Maxilla (Figures 81-84) with apex of lacinia truncate with well developed "spore brush", spines more or less numerous and long; setae on inner face of lacinia numerous to few, scattered or in a single irregular row; inner face of lacinia with a few spines on margin proximal to spore brush; galea with apical setae in numerous close rows, setae filiform. Labium (Figures 105-107) with ligula broadly rounded, entire; medial setae 2.

*Thorax*. – Pronotum moderately transverse, 1.6 to 1.9 times as wide as long; convex, antero-lateral margins strongly deflexed in some; apical angles and anterior margin broadly rounded; posterior angles obtuse; posterior margin very slightly or not at all bisinuate, emarginate medially; sculpture reticulate or obsoletely reticulate; microsetae moderate in size or long and silky, densely arranged; macrosetae small to obsolete. Elytra with apico-lateral angles not sinuate, setae long, silky, densely arranged; punctures small or large, uniformly distributed. Prosternum slightly transverse, with very slight transverse carina or carina absent; without medial knob, carina or protuberance. Mesosternum broad in front of coxae; with marked medial longitudinal carina or carina absent or with low difuse ridge medially. Mesosternal process very wide, extended to posterior margin of middle coxal cavities, apex truncate. Metasternal process not or very slightly extended between coxal cavities. Suture between meso- and metasternal processes complete, not fused, slightly beaded in some, or more or less fused. Metepisternum with setae numerous, in 2 or more irregular rows or single row anteriorly and 2 irregular rows posteriorly; setal punctures large, conspicuous, or moderate in size; setose area in deep groove or not, with slight antero-ventral carina or not. Tarsomere 1 of hind tarsus 1.3 to 2.0 times as long as 2; with or without ventro-lateral ctenidium.

*Abdomen*. – Broadly oval, elongate oval or more or less parallel-sided in dorsal aspect; more or less densely pubescent. Terga 3-5 slightly transversely impressed. Sterna not modified. Tergum 7 modified for openings to abdominal gland ducts. Tergum 10 (Figure 168) with setal patch more or less square; setae numerous, not flattened.

*Aedeagus*. (Figure 202, 203) – Median lobe with apical process small, laterally flattened, blade-like or reduced; flagellum long, exerted, whip-like. Parameres not extensively modified, or apical process with accessory setae.

*Spermatheca*. – (Figure 184) Neck elongate proximal to plate-like flange, or neck elongate and coiled and flange obsolete.

*Secondary sexual characters*. – Posterior margin of tergum 8 of male broadly, shallowly emarginate. Female unmodified, or broadly, shallowly emarginate.

Discussion. – Except for the broad, entire ligula and general habitus similarities, New World species of *Brachida* described by Sharp (1883) share few characteristics with Old World *Brachida* as typified by *B. notha* (Erichson) and *B. exigua* Heer. Two medial setae on the labium, accessory teeth on the inner face of the lacinia, more rows of setae on the galea, and very different form of secondary sexual characteristics and median lobe of the aedeagus, seem to warrant placing the New World *Brachida* in a separate genus. The taxon *Probrachida* new genus is here proposed to contain these New World species. It is possible that *Probrachida* might prove to be a subgenus of *Brachida* Mulsant and Rey with additional study. However, available data do not support this conclusion. In particular, the different number of medial setae on the labium and very different forms of the median lobe of the aedeagus of members of these two taxa suggest that they are not very closely related.

Relationships of *Probrachida* are not well understood. In mouthpart structure, members of *Probrachida* are more plesiotypic than any other gyrophaenine. *Probrachida* may be the sister group to all other Gyrophaenina (Figure 252) or the sister group to *Brachida* (Figure 253). If the latter, then *Probrachida* and *Brachida* together would form the sister group to all other Gyrophaenina.

*Type species*. – *Brachida modesta* Sharp 1883:265 is here designated as the type species of *Probrachida* new genus. *B. modesta* is chosen for two reasons: it appears first in the text (Sharp 1883) and there are more specimens in the syntype series of this species (15 specimens, including both males and females) than for any other member of the genus. The syntype series is in the collection of the British Museum (Natural History).

*Included species*. – The following species are transferred from *Brachida* Mulsant and Rey to *Probrachida* new genus:

*Probrachida batesi* (Sharp 1876:49) new comb.,
*Probrachida carinata* (Sharp 1883:266) new comb.
*Probrachida geniculata* (Sharp 1883:266) new comb.
*Probrachida modesta* (Sharp 1883:265) new comb.
*Probrachida reyi* (Sharp 1876:49) new comb.
*Probrachida sparsa* (Sharp 1883:266) new comb.

*Brachida importuna* Erichson (1839-40) from Colombia, *B. sexalis* Bernh. (1922) from Bolivia, and *B. tumidula* Erichson (1839-40) from Colombia may also belong to *Probrachida*, but I have not had opportunity to examine specimens of these species.

*Natural history*. – Nothing is known of the natural history of members of *Probrachida*.

*Immature stages*. – Undescribed.

*Distribution*. – Species of *Probrachida* are known only from the New World tropics or subtropics. Four species are known from Central America, and two from the Amazon region.

*Major literature*. – Species here included in *Probrachida* have not been discussed except in the original descriptions by Sharp (1876, 1883). Sharp's descriptions are superficial and he provides no keys to species or figures of structural features.

### 3.3.3.6 *Brachida* Mulsant and Rey

(Figures 15, 42-46, 65, 85-87, 108, 109, 158, 185, 204-206, 225)

*Brachida* Mulsant and Rey 1872:94. Type species: *Brachida notha* (Erichson) (from *Homalota*). Fixed by Mulsant and Rey 1872:94 by monotypy.

Mulsant and Rey 1872:94. Fauvel 1872:646. Gangelbauer 1895:305. Casey 1906:279. Reitter 1909:86. Fenyes 1918:92. Cameron 1939:50. Lohse 1974:26.

*Diagnostic combination*. – More or less robust, elongate-oval in dorsal aspect. Body macrosetae long, more or less silky, body markedly pubescent. Head deflexed into more or less oblique plane; base covered by anterior margin of prothorax. Pair of macrosetae present on vertex of head. Maxilla with setae on inner face of lacinia numerous, in single row or scattered; inner face of lacinia without teeth; setae on apex of galea in numerous to few close rows, etae unmodified, filiform. Labium with ligula broadly rounded, entire. Spermatheca (Figure 185) and aedeagus (Figure 204-206) form distinctive.

*Description*. – Length of adult 1.5 to 2.7 mm. Body robust, elongate-oval in dorsal aspect. Surface sculpture reticulate or smooth; integuments shining to subshining. Microsetae long, silky, densely arranged and body very pubescent, or microsetae shorter and body slightly pubescent; punctures small to moderate.

*Head*. (Figure 15) – Slightly transverse, oval, deflexed into more or less oblique plane; microsetae numerous, closely arranged, long or short; Macrosetae pair on vertex or not, setae large, conspicuous, or small, inconspicuous. Infraorbital carina complete, well developed. Neck carina slightly developed. Antenna various, as long as head and pronotum together, to as long as head, pronotum and 1/2 elytra together. Antennomere 4 elongate, quadrate or slightly transverse; 5-10 elongate or more distal antennomeres subquadrate to quadrate.

*Mouthparts*. – Labrum (Figures 42-46) with major setae well developed or difficult to distinguish from numerous accessory setae. Lateral sensilla rows of 3 to 5 spiniform sensilla, near to slightly distant from lateral margin; medial sensory area with sensilla well developed. Mandibles (Figure 65) with left bifid at apex or not, right not bifid; right with well developed internal tooth. Prostheca typical of subtribe or medial internal fringe with processes spiniform rather than bifid. Maxilla (Figures 85-87) with apex of lacinia obliquely truncate, with well developed "spore brush"; setae on inner face of lacinia numerous to few, in single row or scattered; inner face of lacinia without teeth, with 2 to 3 hyaline sensilla; galeal setae in few to numerous close rows, setae filiform, not flattened. Labium (Figure 108, 109) with ligula entire, produced as broadly rounded lobe; medial seta 1.

*Thorax*. – Prothorax moderately transverse, 1.6 to 1.9 times as wide as long, convex, anterior angles and sides depressed; hypomera not visible in later aspect; more or less broadly oval in dorsal aspect; posterior margin not bisinuate to very slightly sinuate, emarginate medially or not; sculpture reticulate, obsoletely reticulate or smooth; microsetae numerous, long to more or less short, densely arranged; macrosetae large, conspicuous, to small, inconspicuous, or obsolete. Elytral apico-lateral angles not to slightly sinuate. Prosternum slightly to moderately transverse, with or without slight transverse ridge; without medial knob, carina or protuberance. Mesosternum broad in front of coxae, without medial longitudinal ridge along midline. Mesosternal process long, reaching apex of middle coxal cavities, apex truncate or slightly emarginate. Metasternal process extended slightly between middle coxal cavities or not. Suture between meso- and metasternal processes complete, not fused. Metepisternum (Figure 158) with setae numerous, scattered, or in 2 irregular rows; setose area not margined antero-ventrally by carina or with faint carina. Tarsomere 1 of hind tarsus 1.3 to 2.0 times as long as 2; with ventro-lateral ctenidium.

*Abdomen*. – Elongate oval in dorsal aspect, robust; more or less densely pubescent or with few scattered setae. Terga 3-5 or 3-6 moderately to slightly transversely impressed. Sterna not modified. Anterior margin of tergum 7 modified for openings to abdominal gland ducts. Tergum 10 with setal patch more or less square; setae numerous, not flattened.

*Aedeagus*. (Figures 204-206, 225) – Distinctive; median lobe with apical process small; flagellum long, slender, coiled internally within median lobe.

*Spermatheca*. (Figure 185) – Distinctive; typical of subtribe, neck elongate, coiled distal to lateral flange.

*Secondary sexual characteristics*. – Males with posterior margin of tergum 8 broadly sinuate or emarginate. lateral margins of sinuation produced as spines or not; sinuation with or without medial spinose processes; tergum 7 with or without slight medial knob. Females unmodified.

*Discussion*. – *Brachida* Mulsant and Rey badly needs comprehensive study on a world-wide basis. A large number of species have been described from all parts of the world except America north of Mexico. I think that all New World species should be in the genus *Probrachida* (see disscussion under that genus). It is uncertain which of the remaining described species should be included in *Brachida*. It appears from the very distinctive autapotypic structure of the spermatheca and median lobe of the aedeagus, that the group characterized by these features is monophyletic. I have examined specimens of a number of species of *Brachida* from widely separate localities and found the distinctive features of these characters to be uniform. Therefore, I think that many of the described species should be included in the same genus as the European forms of *Brachida*. However, it also appears that many species have been incorrectly assigned to *Brachida*. For example, *Brachida elevata* Fauvel is a *Sternotropa* and *Brachida zealandica* Bernh. is not a gyrophaenine (10-articled antenna indicates that it should probably be placed in the tribe Oligotini).

Relationships of *Brachida* are uncertain. It may be hypothesized to be either the sister group to *Probrachida*, or the sister group to the "Sternotropa" + "Gyrophaena" lineages. Members of *Brachida* are highly autopotypic in many structural features (including spermathecal and aedeagal structure) and relatively plesiotypic in mouthpart structure (particularly structure and arrangement of setae on the galea and lacinia of the maxilla; see Section 4.2.2.5 for a detailed discussion).

*Natural history*. - Little is known of the natural history of species of *Brachida*. They are occasionally found on fungi (usually associated with wood) (Benick 1952), but Lohse (1974) gives the habitat of *Brachida exigua* Heer as grass tufts and ground litter, and Cameron (1939) states that specimens of *Brachida* are found in moss and dead leaves in addition to fungi.

*Immature stages*. – Undescribed.

*Distribution*. – If New World forms of *Brachida* are moved to *Probrachida*, then the numerous remaining species are found throughout the Old World. Species are known from Europe, Africa, India, Southeast Asia, Japan, New Caledonia, Australia and New Zealand.

*Major literature*. – There is no comprehensive discussion with complete keys and descriptions of species of *Brachida* of any region except India (Cameron 1939) and Europe (Lohse 1974, Likovsky 1964, and others).

### 3.3.3.7 *Agaricochara* Kraatz

(Figures 16, 47, 66, 88, 95, 110, 126, 146, 152, 169, 186, 207, 226, 242, 249)

*Agaricochara* Kraatz 1856:361. Type species: *Agaricochara laevicollis* Kraatz. Fixed by Kraatz 1856:361 by monotypy.

Kraatz 1856:361. Mulsant and Rey 1871:90. Gangelbauer 1895:304. Casey 1906:278. Reitter 1909:85. Fenyes 1918:92. Scheerpeltz 1930:70. Seevers 1951:740. Lohse 1974:130. White 1977:304. Seevers 1978:163.

*Diagnostic combination*. – Small beetles, adults 1.2 to 1.5 mm in length; surfaces reticulate, with short pubescence throughout. Head almost round in dorsal aspect, 1.1 times as wide as long. Pronotum moderately transvere, 1.6 to 1.7 times as wide as long. Mesosternum with medial longitudinal carina to 1/2 distance to apex of mesosternal process. Mesosternal process extended 2/3 distance to base of middle coxae, separated from metasternal process by very short isthmus; Ms.P:I:Mt.P=7:0.5:4. Maxilla with setae on inner face of lacinia numerous, scattered; setae on apex of galea in 4 distinct rows, setae flattened. Labium with ligula protruded, parallel-sided, bifid 1/3 to 1/2 distance to base;' medial seta 1. Aedeagus form distinctive (Figure 207).

*Description*. – Small beetles, adults 1.2 to 1.5 mm in length; more or less flattened and parallel-sided. Sculpture reticulate throughout; integument subshining to dull. Macrosetae short, more or less densely arranged throughout; punctures small to moderate.

*Head*. (Figure 16) – Round to slightly transverse in dorsal aspect, 1.0 to 1.1 times as wide as long; not or slightly deflexed to oblique plane; tempora large, broadly rounded to base of head; microsetae numerous, short, more or less densely arranged; macrosetae absent. Eyes moderate in size. Infraorbital carina present, slightly developed. Neck carina present, slightly developed. Antenna longer than head and prothorax together; antennomeres 4 similar to

1-3, elongate; 5-7 longer than wide; 8-10 subquadrate to quadrate.

*Mouthparts*. — Labrum (Figure 47) with major setae distinct; without accessory setae. Lateral sensilla row with 2-4 slightly developed spiniform sensilla, distant from lateral margin; medial sensory area with sensilla well developed. Mandibles (Figure 66) not bifid at apex; right with slight internal tooth. Prostheca typical of subtribe. Maxilla (Figure 88) with apex of lacinia obliquely truncate, with well developed spiniform "spore brush", teeth small, close densely arranged; setae on inner face of lacinia more or less numerous, scattered; setae on apex of galea in 4 distinct rows, setae flattened. Labium (Figure 110) with ligula protruded, parallel-sided, bifid 1/3 to 1/2 distance to base, medial seta 1.

*Thorax*. — Prothorax (Figure 126) moderately transverse, 1.6 to 1.8 times as wide as long, slightly convex; antero-lateral angles slightly depressed; hypomera very narrowly visible in lateral aspect or not; posterior margin slightly bisinuate, not emarginate medially; sculpture reticulate; microsetae numerous, small, uniformly and densely distributed; macrosetae small, inconspicuous. Elytral apico-lateral angles not or slightly sinuate. Prosternum (Figure 146) moderately transverse, with fine transverse carina; without medial knob, carina or protuberance. Mesosternum with moderate medial longitudinal carina to 1/2 distance to apex of mesosternal process.

Mesosternal process extended 2/3 distance to base of middle coxae, separated from metasternal process by a very short isthmus; Ms.P:I:Mt.P ratio = 7:0.5:4. Metepisternum with setae in single row, margined antero-ventrally by slight carina. Tarsomere 1 of hind tarsus 1.2 to 1.3 times as long as 2, with slight ventro-lateral ctenidium of 6 to 7 setae.

*Abdomen*. – Parallel-sided or sides slightly convergent from base to apex. Terga 3-5 moderately to slightly transversely impressed. Sterna not modified. Anterior margin of tergum 7 modified for opening to abdominal gland ducts. Tergum 10 (Figure 169) with setal patch more or less square; setae short, setiform or slightly flattened.

*Aedeagus*. (Figure 207) – Distinctive. Median lobe with apical process large, elongate; flagellum hook-like, more or less sclerotized. Apical sclerite of paramere elongate (Figure 226).

*Spermatheca*. (Figure 186) – Typical of subtribe, simple.

*Secondary sexual characteristics*. – Males with tergum 8 broadly sinuate; lateral margins of sinuations produced as spines-like processes; sinuation with a small denticle on each side of midline.

*Discussion*. – The concept of the genus *Agaricochara* is considered here in a very resticted sense in comparison to that of Seevers (1951) and White (1977). Inclusion of a number of New World species within *Agaricochara* Kraatz as done by Seevers (1951), and inclusion of the subgenus

*Phaenogyra* Mulsant et Rey of *Gyrophaena* as done by White (1977) makes *Agaricochara* a polyphyletic assemblage. In the restricted sense considered here, *Agaricochara* is made up of only two European species, *A. laevicollis* Kraatz and *A. aspera* Fauvel. Similarities in the aedeagus of these two species, in addition to other shared character states, provide strong evidence that these two form a monophyletic group. Members of the subgenus *Phaenogyra* are certainly members of *Gyrophaena* rather than *Agaricochara*, as indicated by the protruded, undivided ligula of members of *Phaenogyra*. Seevers (1951) described several species of North American gyrophaenines as *Agaricochara*. He based his concept of *Agaricochara* principally on antennal structure and presence of a markedly transverse pronotum. However, among those species placed in *Agaricochara*, Seevers included some which have members with an entire ligula (*e.g.*, *G. hubbardi* Seevers) and some which have members with a divided ligula (*e.g.*, *G. apachaena* Seevers). The North American species with divided ligulae appear to be more closely related to *Sternotropa* Cameron and *Brachycara* Sharp than to *Agaricochara* Kraatz, and they differ substantially in aedeagal structure from the latter. I have, therefore, removed these North American species from *Agaricochara* (see discusion under *Agaricomorpha* new genus).

Relationships of *Agaricochara* are uncertain. The most parsimonious arrangement at present is inclusion of this genus in the "Sternotropa" lineage based on the hypothesis that the divided ligula of these taxa is a synapotypy. However, this placement requires considerable parallel development of apotypic conditions with members of the "Gyrophaena" lineage. (See discussion in Sections 4.2.2.7.1 and 4.2.2.8.1 for a more detailed discussion of this problem.)

*Natural history*. – Members of *Agaricochara* are most commonly found in association with fleshy or leathery polypore mushrooms on logs (Donisthorpe 1935, Scheerpeltz and Höfler 1948, Benick 1952).

*Immature stages*. – White (1977) described larva of *A. laevicollis* Kraatz.

*Distribution*. – The two species in this genus are known from Europe.

*Major literature*. – No comprehensive discussion of members of *Agaricochara* is available, but *A. laevicollis* is well described and illustrations of structural features are available in Lohse (1974), Seevers (1951), Scheerpeltz and Höfler (1948) and included references.

### 3.3.3.8 *Sternotropa* Cameron

(Figures 17, 48-50, 67-69, 89-91, 111, 112, 127, 135, 147, 153, 170, 171, 187, 208, 209, 227, 228)

*Sternotropa* Cameron 1920:220. Type species: *Sternotropa nigra* Cameron 1920:220. Fixed by Blackwelder 1952:360 by subsequent designation.

Cameron 1920:220. Cameron 1939:142.

*Diagnostic combination*. – Small beetles (adults 1.1 to 1.7 mm in length); body form slightly limuloid, sides of abdomen convergent to more or less pointed apex; body moderately to slightly pubescent, microsetae more or less uniformly distributed. Pronotum markedly transverse, 1.8 to 2.1 times as wide as long. Pronotum posterior margins markedly bisinuate. Mesosternum with medial longitudinal carina, complete or obsolete in apical 1/3. Mesosternal process extended to middle or slightly posterior to middle of mid-coxae; suture between meso- and metasternal processes complete or more or less fused. Maxilla with setae on inner face of lacinia numerous or few, in single row or scattered; setae on apex of galea in 4 well separated rows, setae flattened. Labium with ligula bifid, divided almost to base. Aedeagal form distinctive (Figure 208, 209).

*Description*. – Length 1.1 to 1.7 mm. Body broadest near middle of elytra, abdomen tapered to more or less pointed apex; flattened to slightly robust; sculpture reticulate to smooth, integuments shining to subshining; sparsely to moderately to more or less densely pubescent;

microsetae short to moderate, fine, more or less uniformly distributed; punctures fine to very fine, asperite or not; macrosetae small, inconspicuous, obsolete, or large and conspicuous.

*Head*. (Figure 17) – Transverse to markedly transverse; held more or less in plane of body to slightly inclined; sculpture reticulate to smooth; microsetae short, moderately numerous to sparse, uniformly distributed; punctures fine to minute; macrosetae absent. Eyes moderate in size. Infraorbital carina present, markedly to moderately developed, complete or obsolete antero-ventrally. Neck carina present, more or less slight, obsolete ventrally. Antenna with antennomere 4 similar in setation and general shape to 1-3, and subquadrate transverse; 5 slightly elongate, quadrate or transverse; 6-10 more or less transverse.

*Mouthparts*. – Labrum (Figures 48-50) with major setae well developed,without accessory setae; lateral sensilla row with 1-3 slightly developed spine-like sensilla, or sensilla row absent; sensilla of medial sensory area well developed. Mandibles (Figures 67-69) typical of subtribe; not bifid at apex; right mandible with small internal tooth or tooth obsolete. Maxilla (Figures 89-91) with apex of lacinia obliquely truncate, more or less broad, with well developed "spore brush"; teeth of spore brush small, very numerous and densely arranged; inner face of lacinia with single irregular row of moderately sized setae, or setae more or less scattered; 2 or 3 large hyaline setiform sensilla present or absent, galea with apical setae in 4 distinct rows, setae subspatulate to plate-like. Labium (Figure 111, 112) with ligula bifid, divided almost to base; and broadly pointed apically or sides converged to sharp point apically. Medial seta 1.

*Thorax*. – Prothorax (Figure 127) markedly transverse, approximately 2.0 times as wide as long; slightly to moderately convex in cross-section, sides moderately depressed, anterior angles depressed; hypomera not visible in lateral view; anterior border straight or broadly rounded; latero-apical angles obtusely angulate or broadly rounded; sides broadly convergent from near baseo-lateral angles to apico-lateral angles; posterior border moderately to markedly bisinuate, not emarginate medially; sculpture reticulate to smooth, integuments subshining to shining; microsetae moderate to numerous, sparse to densely, uniformly distributed; punctures small to fine, asperite or not; macrosetae very small, inconspicuous or obsolete on disc, or one or more lateral setae more or less large and conspicuous. Elytra (Figure 135) with sutural length equal to or slightly less than pronotal length. Outer apical angles moderately to markedly sinuate; integument reticulate to smooth, subshining to shining; microsetae small, moderate to numerous, sparse to moderately densely, uniformly distributed; macrosetae very small, obsolete or lateral 2 to 3 setae large, conspicuous. Prosternum (Figure 147) transverse, without faint transverse carina; with medial knob, protuberance or spine. Mesosternum with medial longitudinal carina, complete to apex of mesosternal process or more or less obsolete in apical 1/3. Mesosternal process moderately broad, extended between middle coxal cavities to middle or slightly posterior to middle of coxal cavities. Metasternal process extended anteriorly to broad contact with mesosternal process; suture complete, or, in specimens of most species, more or less fused and indistinct (Figure 153); isthmus absent. Metepisternum with setae few to moderately numerous, scattered in 1 or 2 irregular rows; setose area not delimited by fine carina. Hind tarsus with tarsomere 1 1.0 to 1.5 times as long as 2.

*Abdomen*. – Flattened to slightly robust, sides more or less convergent from broad base to narrow apex; terga not transversely impressed (slightly developed carina present or not on 3-5), or 3-6 more or less slightly impressed. Tergum 10 (Figure 170, 171) with medial setose patch chevron-shaped; setae in 2 distinct oblique rows (third indistinct row present in some); rows convergent to point proximally or setae more numerous and in 3-4 well developed rows.

*Aedeagus*. (Figure 208, 209) – Similar to that found among species of *Pseudoligota*. Apical lobe highly modified and complex or not; flagellum long, slender, whip-like; emerging near base of median lobe, curved proximally and extended apically in a groove in functionally ventral surface. Parameres (Figures 227, 228) with 2 setae of apical sclerite enlarged, near base of sclerite.

*Spermatheca*. (Figure 187) – Typical of subtribe; unmodified, simple.

*Secondary sexual characteristics*. – Various. Males with posterior margin of tergum 8 broadly to narrowly emarginate, lateral margins of emargination more or less prolonged as blunt teeth or not, emargination medially with or without one or more small teeth or lobes; tergum 7 with pair of small spines medially or not. Female unmodified or with posterior margin of tergum 8 with 2 short, blunt teeth separated by broad semicircular emargination.

*Discussion*. – *Sternotropa* Cameron is most closely related to *Pseudoligota* Cameron, as indicated by similarities in the median lobe of the aedeagus (see discussion in Section 4.2.2.7.2) and has close, but uncertain, affinities with *Adelarthra* Cameron.

*Natural history*. – No information about natural history of *Sternotropa* is available. Based on structure of the spore brush of the maxilla, and habitat preferences of related gyrophaenines (see Table 4), it is likely that members of *Sternotropa* are most common on fleshy or leathery polypore mushrooms.

*Immature stages*. – Undescribed.

*Distribution*. – Members of *Sternotropa* are known from India, Southeast Asia, Fiji, Sumatra and Malaya.

*Major literature*. – Cameron (1939) gives keys and descriptions for the Indian species.

### 3.3.3.9 *Pseudoligota* Cameron

(Figures 18, 51, 52, 70, 92, 113, 128, 136, 154, 159, 172, 173, 188, 210, 211, 229)

*Pseudoligota* Cameron 1920:213. Type species: *Pseudoligota varians* Cameron 1920:213. Fixed by Blackwelder 1952:327 by subsequent designation.

Cameron 1920:213. Cameron 1939:145.

*Diagnostic combination*. – Minute to very small (adults 0.8 to 1.2 mm in length). Body slightly limuloid, widest at base of thorax, sides of abdomen converging from base to apex. Body moderately to slightly pubescent, microsetae short, uniformly distributed. Pronotum moderately to markedly transverse, 1.8 to 2.0 times as wide as long; slightly to moderately convex in cross section; hypomera not visible in lateral aspect; posterior margin moderately to slightly bisinuate. Eltyral apico-lateral angles slightly to moderately sinuate. Mesosternum without medial longitudinal carina. Meso- and metasternal processes fused and indistinguishable. Maxilla with inner face of lacinia with single row of setae; setae on apex of galea in 4 widely separated rows, setae flattened, subspatulate. Labium with ligula bifid, divided 2/3 to 3/4 distance to base; medial seta 1. Aedeagal form distinctive (Figure 210, 211).

*Description*. – Minute to very small beetles, adult length 0.8 to 1.2 mm. Body slightly limuloid; widest at base of thorax, broadly rounded to head anteriorly, sides of abdomen converging from base to apex or not; slightly robust to not robust. Body sculpture reticulate to smooth; integuments dull to shining. Body moderately to more or less markedly pubescent, microsetae short, more or less closely spaced and uniformly distributed, punctures small to minute, asperite or not; macrosetae very small, inconspicuous, apparently absent from specimens of some species.

*Head*. (Figure 18) – Transverse, more or less broadly oval in cross-section, more or less inclined ventrally from plane of body. Sculpture reticulate to smooth. Microsetae short, numerous, uniformly distributed; punctures fine to minute; macrosetae absent. Eyes moderate in size. Infraorbital carina slightly developed, complete ventrally or obsolete antero-ventrally. Neck carina slight, obsolete ventrally. Antenna with antennomere 4 similar to 1-3; antennomeres 4-10 transverse, each more so than the preceding.

*Mouthparts*. – Labrum (Figure 51, 52) without accessory setae; lateral sensilla row absent; sensilla of medial sensory area well developed. Mandibles (Figure 70) typical of subtribe; not bifid at apex, right with small tooth internally or tooth obsolete. Maxilla (Figure 92) with apex of lacinia obliquely truncate with well developed "spore brush"; teeth of spore brush small, numerous, densely arranged; inner face of lacinia with single row of moderately sized setae and 2 or 3 large, hyaline setiform sensillae; galea with apical setae in 4 well separated rows, setae subspatulate to plate-like. Labium (Figure 113) with ligula bifid, divided 2/3 to 3/4 distance to base; lobes of ligula short, sides converging to point apically. Medial seta 1 or absent.

*Thorax.* (Figure 128) – Pronotum markedly transverse, 1.8 to 2.0 times as wide as long; slightly to moderately convex in cross-section; sides moderately depressed; hypomera not visible in lateral aspect; anterior border straight, apical angles more or less obtusely angulate; posterior border moderately to slightly bisinuate, not emarginate medially; sculpture reticulate or smooth, integuments dull to shining; microsetae short, numerous, more or less densely and uniformly distributed; punctures fine to minute, asperite or not; macrosetae very small, inconspicuous, or absent. Elytra (Figure 136) equal to or shorter than pronotal length; apico-lateral angles moderately to slightly sinuate; integument reticulate to smooth, dull to shining; microsetae small, numerous, densely and uniformly distributed; punctures very fine, asperite or not; macrosetae very small, inconspicuous or absent. Prosternum transverse to markedly transverse; without transverse carina; with or without low medial knob or protuberance. Mesosternum without medial longitudinal carina. Mesosternal process moderately broad, extended between middle coxal cavities and fused to metasternal process, processes indistinguishable (Figure 159) Middle coxal cavities moderately separated. Metepisternum with setae moderately numerous, in 2 irregular rows; setose area not delimited by fine carina. Hind tarsus with tarsomere 1 about as long as 2; ventro-lateral edge with ctenidium of 4 to 6 setae.

*Abdomen*. – Flattened to slightly robust, sides slightly to moderately convergent from base to apex. Terga not transversely impressed with indistinct transverse carinae on 3-5. Tergum 10 (Figure 172, 173) with medial setose patch square (Figure 173) or with posterior edge broadly incised (Figure 172); setae short, stubby, not flattened.

*Aedeagus*. (Figure 210, 211) – Distinctive. Median lobe with flagellum emergent near base of bulb, curved proximally around base of median lobe, and extended apically in groove in functionally ventral surface. Parameres (Figure 229) with 2 proximal setae of apical sclerite enlarged, near base of sclerite.

*Spermatheca*. (Figure 188) – Typical of subtribe; unmodified, simple.

*Secondary sexual characteristics*. – Males with posterior margin of tergum 8 with broad blunt tooth; tergum 7 with faint median longitudinal carina or not; elytra strongly asperite distally near suture and/or near lateral margin or not. Female unmodified or with posterior margin of tergum 8 with broad lobe.

*Discussion*. – Many members of *Pseudoligota* are among the smallest aleocharines and thus among the smallest beetles.

*Pseudoligota* is most closely related to *Sternotropa* and *Adelarthra* (see discussion under *Sternotropa* and in Section 4.2.2.7.2).

*Natural history*. – Cameron (1939) reports that members of some species of *Pseudoligota* have been found on "Polyporus". A few specimens have been collected on rotting fruit, in rotting fungus, and under bark (label data).

*Immature stages*. – Undescribed.

*Distribution*. – Known from India and Southeast Asia.

*Major literature*. – Cameron (1939) provides a key to and descriptions of the Indian species.

### 3.3.3.10 *Neobrachida* Cameron

(Figure 115)

*Neobrachida* Cameron 1920:51. Type species: *Neobrachida castanea* Cameron 1920:51. Fixed by Cameron 1920:51 by monotypy.

Cameron 1920:51. Cameron 1939:55.

*Diagnostic combination*. – Length of adult 2.3 mm. Body more or less parallel-sided; sculpture smooth, integuments markedly shining; body sparsely pubescent, microsetae small, number and distribution different on different areas of body. Pronotum moderately transverse, 1.7 times as wide as long, slightly convex in cross-section; sides moderately convex, hypomera not visible in lateral aspect; pronotal posterior margin slightly bisinuate. Elytral apico-lateral angles moderately bisinuate. Mesosternum with diffuse, low, medial longitudinal carina. Mesosternal process extended to posterior 1/3 of mid-coxal cavities. Metasternal process extended between coxae, truncate at contact with mesosternal process; suture between meso- and metasternal processes complete, unmodified. Labium with ligula elongate, as long as first palpomere, parallel-sided, bifid in apical 1/3; lobes of ligula narrow, pointed, divergent. Medial seta 1.

*Description*. – Length of adult 2.3 mm. Body more or less parallel-sided, sides convergent slightly posteriorly; more or less flattened, not robust; sculpture smooth, integuments markedly shining; sparsely pubescent; microsetae small, fine, number various on different body regions;

punctures very fine; macrosetae various on different body regions, small, inconspicuous, or large and conspicuous.

*Head*. – Transverse; microsetae small, very sparse; punctures very fine; macrosetae absent. Infraorbital carina moderately developed, complete ventrally. Neck carina well developed. Antenna with antennomere 4 similar in setation and general shape to 1-3; antennomere 4 transverse; 5-10 transverse, each slightly wider than preceding, antenna slightly incrassate from antennomere 4 to apex.

*Mouthparts*. – Labrum not observed. Mandibles not observed. Maxilla with apex of lacinia truncate, with well developed "spore brush"; teeth numerous and closely spaced; galea not observed. Labium (Figure 115) with ligula slender, elongate, almost as long as palpomere 1, parallel-sided, bifid in apical 1/3, lobes narrow, pointed, divergent. Medial seta 1.

*Thorax*. – Prothorax moderately transverse, 1.7 times wider than long; slightly convex in cross-section, sides moderately depressed; hypomera not visible in lateral view; anterior border broadly rounded; latero-apical angle broadly rounded; posterior border slightly bisinuate; microsetae small, sparse, uniformly distributed; punctures very fine; macrosetae small, inconspicuous except L3 large and conspicuous. Elytra at suture longer than pronotal length. apico lateral angles moderately sinuate; microsetae sparse, uniformly distributed, punctures fine; three lateral macrosetae large, conspicuous. Prosternum moderately transverse, without transverse carina; with medial protuberance. Mesosternum without medial longitudinal carina, but low diffuse ridge along midline; ridge extended to apex of mesosternal process. Mesosternal process extended to posterior third of mid-coxal cavities. Metasternal process truncate at contact with mesosternal process; the suture complete, unmodified. Isthmus absent. Metepisternum with setae numerous, scattered in 2 irregular rows; setose area not delimited below by carina. Hind tarsus with first tarsomere 1.4 times as long as second.

*Abdomen*. – Sides subparallel, very slightly convergent from base to obtusely rounded apex. Terga 3-5 (6 faintly) with moderate to slight transverse impressions. Tergum 10 with medial setose patch chevron-shaped; setae in 2 distinct oblique rows convergent to point proximally (similar to Figure 170).

*Aedeagus*. – Unknown.

*Spermatheca*. – Unknown.

*Secondary sexual characteristics*. – Male unknown. Female with posterior margin of tergum 8 broadly emarginate medially.

*Discussion*. – Only a single specimen, a female, of *Neobrachida* is known. It, therefore, was not possible to do dissections required for detailed examination of many structural features. The spermatheca is visible through the sides of the abdomen, but it is not possible to determine detailed structure.

Relationships of *Neobrachida* are uncertain. The divided ligula seems to place it in the "Sternotropa" lineage and structure of the setal patch on tergum 10 suggests it may be related to *Sternotropa*. However, more precise relationships cannot be resolved at present (see Section 4.2.2.7.4).

*Natural history*. – Unknown.

*Immature stages*. – Undescribed.

*Distribution*. – Only known specimen from Ceylon.

*Major literature*. – *Neobrachida* is only known from descriptions by Cameron (1920, 1939).

### 3.3.3.11 *Adelarthra* Cameron

(Figures 53, 93, 114, 212, 230, 231)

*Adelarthra* Cameron 1920:222. Type species: *Adelarthra barbari* Cameron 1920:222. Fixed by Cameron 1920:222 by monotypy.

Cameron 1920:222.

*Diagnostic combination*. – Small beetles (adults 1.1 to 1.2 mm in length); body form slightly limuloid, broadest near middle of elytra, sides convergent posteriorly to apex of pointed abdomen; moderately robust; sculpture smooth throughout, integuments shining; microsetae small, scattered, body subglabrous; macrosetae on lateral margins of pronotum, elytra, and abdomen extremely large, dark, bristle-like. Pronotum markedly transverse, 1.9 times as wide as long; convex, sides moderately depressed, antero-lateral angles markedly depressed; hypomera not visible in lateral aspect; posterior margins moderately bisinuate. Elytral apico-lateral angles sinuate. Mesosternum with slight medial longitudinal carina. Meso- and metasternal processes broad between coxae; suture between processes fused, indistinguishable. Labium with ligula bifid to base, lobes robust, parallel-sided, rounded apically.

*Description*. – Adult length 1.1 to 1.2 mm. Body sublimuloid, broadest near middle of elytra, broadly rounded anteriorly to head, sides convergent posteriorly to apex of pointed abdomen; moderately robust; sculpture smooth throughout, integuments shining; microsetae small, widely scattered, much of body glabrous, punctures very fine; macrosetae various on different regions of body: small and inconspicuous, or very long, dark and conspicuous.

*Head*. – Markedly transverse; microsetae very few, small, widely scattered, punctures minute; macrosetae absent. Eyes moderate in size. Infraorbital carina moderately developed, complete ventrally. Neck carina present, more or less slight, obsolete ventrally. Antenna with antennomere 4 similar in setation and general shape to 1-3; antennomeres 4-10 slightly transverse, similar in width.

*Mouthparts*. – Labrum (Figure 53) with major setae well developed, without accessory setae; lateral sensilla row with 3-5 small spine-like sensilla, distant from lateral margin; sensilla of medial sensory area well developed. Mandibles not bifid at apex; right mandible with small internal tooth; prostheca typical of subtribe. Maxilla (Figure 93) with apex of lacinia truncate, with well developed "spore brush"; teeth numerous, small and closely spaced; inner face of lacinia with single row of setae, galea with apical setae in 4 distinct rows, setae flattened. Labium (Figure 114) with ligula bifid to base; lobes robust, parallel-sided, rounded apically; medial seta 1.

*Thorax*. – Pronotum (Figure 231) markedly transverse, 1.9 times as wide as long; moderately convex in cross-section; broadest at base, broadly rounded and convergent to anterior angles; sides moderately depressed; antero-lateral angles markedly depressed; hypomera not visible in lateral view; anterior margin and antero-lateral angles broadly rounded; posterior margin bisinuate, not emarginate medially; microsetae absent; macrosetae very small, inconspicuous or obsolete, except L3 prominent. Elytra (Figure 231) transverse, broader at base than pronotum, sutural length equal to pronotal length; elytra shorter at suture than laterally; apico-lateral angles moderately sinuate; microsetae very small, very sparsely and uniformly distributed; macrosetae on lateral margins extremely large, dark and prominant. Prosternum markedly transverse, with transverse carina, carina more prominent, ridge-like medially; medially with marked transverse tooth. Mesosternum with narrow but distinct medial longitudinal carina. Meso- and metasternal processes extended broadly between middle coxal cavities; suture fused, processes indistinguishable. Middle coxal cavities widely separated. Metepisternum bare. Tarsomere 1 of hind tarsus as long as next 2 together.

*Abdomen*. (Figure 231) – Robust, sides convergent from base to slightly pointed apex. Terga 3-6 moderately to slightly transversely impressed. Microsetae few; macrosetae very large, dark, bristle-like. Microsculpture of fine ridges divergent proximally from each setal insertion. Tergum 10 with medial setose patch more or less square, setae few, unmodified. Sterna unmodified.

*Aedeagus*. (Figure 212, 230) – Similar to that found among specimens of *Sternotropa* and *Pseudoligota*.

*Spermatheca*. – Unknown.

*Secondary sexual characteristics*. – Absent.

*Discussion*. – Because of the large dark bristles on the body and the robust sublimuloid body form of members of *Adelarthra*, this is one of the most distinctive taxa among gyrophaenines.

Relationships of *Adelarthra* are uncertain. Similarities in the aedeagus to members of *Sternotropa* and *Pseudoligota* indicate that it shares affinities with these taxa (see Section 4.2.2.7.3 for detailed discussion).

*Natural history*. – Not known. Specimens have been collected from rotten wood and "debris" (label data).

*Immature stages*. – Not described.

*Distribution*. – The two known specimens are from Singapore.

*Major literature*. – Discussed only in original description.

### 3.3.3.12 *Brachycara* Sharp

(Figures 19, 54, 71, 94, 116, 129, 174, 189, 213, 232, 237, 243, 249, 250)

*Brachycara* Sharp 1883:267. Type species: *Brachychara crassa* Sharp 1883:267. Fixed by Fenyes 1918:21 by subsequent designation.

Sharp 1883:267. Fenyes 1918:94. Cameron 1922:637.

*Diagnostic combination*. – Adults 1.8 to 3.0 mm in length. Body form sublimuloid, markedly robust; body moderately to slightly pubescent; microsetae short, stiff, uniformly distributed; integuments shining. Pronotum moderately transverse, 1.5 to 1.8 times as wide as long; very markedly convex, lateral margins markedly deflexed; antero-lateral margins deflexed to vertical; hypomera not visible in lateral aspect; posterior margins bisinuate. Elyral apico-lateral angles markedly sinuate. Mesosternum with slight broad medial longitudinal ridge. Mesosternal process extended to middle or slightly posterior to middle of mid-coxal cavities; suture between meso- and metasternal processes fused. Maxilla with setae on inner face of lacinia scattered; setae on apex of galea in 4 widely separated rows, setae flattened, subspatulate. Labium with ligula bifid to base; lobes broadly separate at base, pointed apically

*Description*. – Adult length 1.8 to 3.0 mm. Body shape sublimuloid, very robust, broadly oval in cross section. Body markedly shining, moderately to slightly pubescent, pubescence stiff, scattered.

*Head*. (Figure 54) – Transverse, oval, deflexed to more or less vertical plane; base hidden in dorsal aspect by anterior margin of pronotum. Shining, without sculpture; moderately pubescent, microsetae short, stiff, widely scattered; punctures small; macrosetae absent. Eyes moderate in size. Infraorbital carina well developed, complete. Neck carina well developed. Antenna various; antennomere 4 similar in setation and general shape to 1-3.

*Mouthparts*. – Labrum (Figure 54) with major setae well developed; with a few scattered accessory setae; lateral sensilla row of 4-5 spine-like sensilla, near lateral margin; slightly sclerotized along midline. Mandibles (Figure 71) not bifid at apex; right mandible with small internal tooth. Prostheca typical of subtribe. Maxilla (Figure 94) with apex of lacinia truncate, very broad, with extensive area of very numerous, small, closely spaced teeth; inner face of lacinia with setae small, numerous, scattered; galea with apical setae in 3 distinct and 1 indistinct (most proximal) rows, rows long, crowded near apex, setae spatulate to plate-like. Labium (Figure 116) with ligula bifid to base; the two lobes widely separated at base, acutely pointed apically. Medial seta 1.

*Thorax*. – Prothorax (Figure 129) markedly transverse, 1.5 to 1.8 times as wide as long; very markedly convex in cross-section, sides markedly depressed, antero-lateral margins depressed to vertical; hypomera not visible in lateral view; anterior margin broadly rounded; hind margins moderately to markedly bisinuate, not emarginate medially; sculpture absent, integuments shining; microsetae short, depressed, widely scattered, more or less uniformly distributed; punctures small; macrosetae very small, inconspicuous. Elytra short, each elytron shorter than wide, longer laterally than at suture; apico-lateral angles markedly sinuate; surface markedly shining; reticulate ground sculpture absent but specimens of some species with punctures united by very fine raised lines; uniformly covered with short appressed microsetae; macrosetae small. Prosternum very short in front of coxae; transverse; with distinct transverse medial knob or protuberance. Mesosternum short, markedly upturned on anterior edge; longitudinal carina absent; medially with slight, broad, longitudinal ridge extended almost to apex of mesosternal process. Mesosternal process extended to just posterior to middle of midcoxal cavities. Metasternal process broadly rounded; suture between meso- and metasternal processes fused, slightly raised as low bead along fusion line. Coxae widely separated (Figure 250). Metepisternum (Figure 249) with setae numerous, 2 or 3 very irregular rows; setose area not delimited by a carina. Tarsomere 1 of hind tarsus as long as next two together.

*Abdomen*. – Robust, broadly oval in cross section; sides convergent from broad base to narrow apex. Terga 3-5 or 3-6 very slightly transversely impressed. Sterna unmodified. Tergum 7 with anterior margin modified as opening of abdominal gland ducts. Tergum 10 (Figure 174) with medial setose patch chevron-shaped, setae in 3 distinct rows; setae flattened, subspatulate.

*Aedeagus*. (Figure 213) – Apical lobe of median lobe elongate, spine-like; flagellum long, slender, whip-like, coiled apically.

*Spermatheca*. (Figure 189) – Typical of subtribe; simple.

*Secondary sexual characteristics*. – Tergum 8 of both male and female modified. Female with tergum 8 broadly incised medially, each lateral edge of incision extended posteriorly as a slight spine; emargination medially with or without a broad slight lobes; Male with tergum 8 deeply emarginate, each lateral edge prolonged as large inwardly curved spine; emargination with large, more or less pointed lobe medially.

*Discussion*. - The very robust, convex, sublimuloid body form, shining integuments, and very extensive "spore brush" of numerous, short, densely arranged teeth make this one of the most distinctive gyrophaenine genera.

Sharp (1883) stated that *Brachycara* was "best located near *Brachida*", but he did not believe that these two taxa were closely related. It appears that *Brachycara* is most closely related to *Agaricomorpha* new genus, and together they form a monophyletic lineage (see Section 4.2.2.7.5).

*Natural history*. - Members of *Brachycara* are most common on fleshy or leatherly polypores on logs. Both larvae and adults have been found on mushrooms of this type (personal observations, and label data).

*Immature stages*. - Not described.

*Distribution*. - Species of *Brachycara* are known from Central America and St. Vincent in the West Indies. There are a number of undescribed species in Mexico and Central America.

*Major literature*. - Known only from original descriptions. Comprehensive keys and illustrations of structural features have not been previously published.

### 3.3.3.13 *Agaricomorpha* new genus

(Figures 20, 28, 55, 72, 95, 117, 130, 140, 148, 155, 160, 175, 190, 214, 215, 236, 242, 248)

*Agaricomorpha* new genus. Type species: *Agaricomorpha apachaena* (Seevers) 1951:743 (from (*Gyrophaena* (*Agaricochara*)). Fixed here by original designation.

Diagnostic combination. – Small beetles (adults 1.0 to 1.6 mm in length). Body more or less flattened to slightly convex; broadest near middle of elytra, sides of abdomen convergent from base to more or less obtusely pointed apex. Head transverse (1.2 to 1.4 times as wide as long); slightly to moderately deflexed, oblique. Pronotum markedly transverse, 1.8 to 2.1 times as wide as long; slightly convex in cross section; lateral margins deflexed, hypomera not visible in lateral aspect; posterior margins moderately to markedly bisinuate, not emarginate medially. Mesosternum with complete, incomplete or without medial longitudinal carina. Mesosternal process extended to slightly posterior to middle, or to posterior 2/3 of mid-coxae; meso- and metasternal processes meeting along broad, truncate suture, or suture fused, processes indistinguishable. Maxilla with setae on inner face of lacinia in single row or scattered; setae on apex of galea in 4 distinct rows, setae flattened, subspatulate. Labium with ligula protruded, parallel-sided, bifid 2/3 to 3/4 distance to base; medial seta 1. Aedeagal form distinctive (Figure 214, 215), median lobe with apical process lateral to origin of flagellum.

*Description*. – Length of adults 1.0 to 1.6 mm. Body more or less flattened to slightly convex; broadest near middle of elytra, abdomen converging to more or less obtusely pointed apex; sculpture reticulate throughout, integuments subshining to dull; microsetae short, more or less densely arranged throughout; punctures small, asperite in many; macrosetae small, difficult to distinguish from microsetae.

*Head*. – (Figure 20) Transverse (1.2 to 1.4 times wider than long); slightly to moderately deflexed to oblique plane; tempora short, rounded to acutely convergent to base of head; microsetae numerous, short, more or less densely and uniformly distributed; macrosetae absent. Eyes moderate in size. Infraorbital carina well developed, or slightly developed antero-ventrally. Neck carina slightly developed. Antenna (Figure 28) longer than head and thorax together; antennomere 4 similar in setation and general shape to 1-3, subquadrate to slightly elongate; 5-7 longer than wide, 8-10 subquadrate, quadrate, or slightly transverse.

*Mouthparts*. – Labrum (Figure 55) with major setae well developed,without accessory setae; lateral sensilla row with 2-5 moderately developed spine-like sensilla, distant form or near lateral margin; sensilla of medial sensory area well developed. Mandibles (Figure 72) not bifid at apex; right with small internal tooth; prostheca typical of subtribe. Maxilla (Figure 95) with apex of lacinia obliquely truncate, with well developed "spore brush"; teeth of spore brush small, close, densely arranged; setae on inner face of lacinia more or less numerous to few, scattered or in single well developed row; galea with apical setae in 4 distinct, clearly separated rows, setae flattened, subspatulate. Labium (Figure 117) with ligula protruded, parallel-sided, bifid 2/3 to 3/4 distance to base; medial seta 1.

*Thorax*. – Prothorax (Figure 130) transverse to markedly transverse (1.8 to 2.1 times as wide as long); slightly convex in cross-section; lateral margins moderatley deflexed, hypomera not visible in lateral aspect; posterior margin moderately to markedly bisinuate, not emarginate medially; microsetae small, numerous, densely and uniformly distributed; macrosetae very small, inconspicuous. Elytral apico-lateral angles moderately to markedly sinuate. Prosternum (Figure 148) transverse, with medial knob, carina or protuberance. Mesosternum with medial longitudinal carina, complete, obsolete or absent in posterior 1/2, or absent. Mesosternal process extended to slightly posterior of middle of, to posterior 2/3 of middle coxal cavities. meso-metasternal the suture broad, truncate, or fused, processes indistinguishable (Figure 155). Metepisternum (Figures 160, 248) with setae in 1 or 2 irregular rows, setose area margined antero-ventrally by slight carina or not. Tarsomere 1 of hind tarsus 1.0 to 1.3 times as long as 2; with slight ventro-lateral ctenidium of 5 to 7 setae.

*Abdomen*. – Sides convergent from base to apex. More or less pubescent, microsetae short. Terga 3-5 moderately to slightly transverse. Sterna not modified. Tergum 7 with anterior margin modified for opening to abdominal gland ducts. Tergum 10 (Figure 175) with medial setose patch chevron-shaped; setae numerous, short, slightly flattened.

*Aedeagus*. (Figure 214, 215) – Distinctive. Median lobe with apical process simple, more or less blade-like, lateral to origin of flagellum. Parameres various, not extremely modified.

*Spermatheca*. (Figure 190) – Typical of subtribe; simple.

*Secondary sexual characteristics*. – Various. Most males with posterior margin of tergum 8 with broad semicircular emargination medially, lateral margins of emargination with small spine-like processes or not. Female with posterior margin of tergum 8 broadly, shallowly emarginate or not, or with margin broadly bisinuate.

*Discussion*. – The taxon *Agaricomorpha* is established here to contain the New World species of *Gyrophaena* (*Agaricochara*) (*sensu* Seevers 1951) with divided ligula. Seevers (1951) based his concept of *Agaricochara* (as a subgenus of *Gyrophaena*) primarily on antennal structure, very transverse pronotum and intercoxal processes which are similar in length. He did not recognize that among those species he included in *Gyrophaena* (*Agaricochara*) were some which have members with entire ligulae, and some with bifid ligulae. Those with an entire ligula should be tentatively included in *Gyrophaena* until that genus has been more thoroughly studied. Among those with bifid ligula, I have argued elsewhere (see discussion under *Agaricochara* Kraatz) that the European *Agaricochara* form a monophyletic group. Members of the New World species with bifid ligula differ from the European *Agaricochara* in form of the median lobe of the aedeagus, and in having a more deeply bifid ligula, chevron-shaped setal patch on tergum 10, more closely joined or fused intercoxal processes, more deeply bisinuate posterior margins of pronotum and more markedly sinuate apico-lateral angles of elytra, and more transverse pronotum. The New World forms seem more closely related to *Sternotropa* and *Brachycara* than to *Agaricochara*. It therefore seems necessary that these forms be placed in a genus separate from the Old World *Agaricochara*.

*Agaricomorpha* appears to be most closely related to *Brachycara* (see Section 4.2.2.7.5).

Type species. – *Gyrophaena* (*Agaricochara*) *apachaena* Seevers 1951:743 is here designated as the type species of *Agaricomorpha* new genus. *G. apachaena* is chosen because it appears to be the first described species of this taxon. Considering the abundance and diversity of members of *Agaricomorpha* in Mexico and Central America, it is suprising that species assignable to this genus were not described by Sharp, Bernhauer or Cameron in their studies of staphylinids from these regions. However, I have had occasion to examine most of the species described by these workers and have not found any assignable to *Agaricomorpha*. The type specimen of

*A. apachaena* is a male in the collection of the California Academy of Sciences.

*Included species*. – The following species are transferred from *Gyrophaena* (*Agaricochara*) (*sensu* Seevers 1951) to *Agaricomorpha* new genus:

*Agaricomorpha apachaena* (Seevers 1951:743) new comb.

*Agaricomorpha ojibway* (Seevers 1951:743) new comb.

In addition, I have seen specimens of a number of undescribed species from Mexico and Central America.

*Natural history*. – Adults and larvae of *Agaricomorpha* have been found on woody and leatherly polypore mushrooms on logs, and appear to be characteristic inhabitants of these mushrooms (personal observations).

*Immature stages*. – Undescribed.

*Distribution*. – The two described species of *Agaricomorpha* are found only in America north of Mexico, one in the southwest and the other in the northeast and north central regions. However, I have seen a number of undescribed species from Mexico and Central America. It seems likely that members of *Agaricomorpha* also occur in South America.

*Major literature*. – Only known from original descriptions by Seevers (1951).

# 4. Evolutionary Analysis of the World Genera of the Subtribe Gyrophaenina

## 4.1 Character Analysis

### 4.1.1 Introduction – Methods and Principles of Character Analysis

The basic process in determination of relationships between taxa is analysis of characters.

Characters or attributes are descriptive terms by which means taxa are identified and described. These characters also provide information about geneological relationships. Hecht and Edwards (1977, p.5) define a character as "a set of limited homologous features that are distributed among two or more taxa." Different expressions of the character among taxa under consideration are called "character states". The suite of character states, assumed to be homologous, is called a "morphocline" or "morphological transformation series". In every morphological transformation series, there is a single ancestral condition, but there can be one or more derived states. Direction of change in a transformation series is called "polarity". Polarity of a transformation series is in a uni- or multidirectional series (Hecht and Edwards 1977).

Effective character analysis resolves into three distinct phases: 1) recognition and description of homologous character states; 2) development of hypotheses about relative usefulness of states of different characters for phylogenetic analysis (character weighting); and 3) development of hypotheses about the polarity of transformation series.

To effectively make hypotheses about relationships of taxa it is necessary to be able to compare structures which are derived from a common ancestral condition; that is homologous character states. When features appear similar in structure and/or development but are not derived from the same common ancestor, the condition is termed homoplasy. Two types of homoplasy occur: that due to parallelism and that due to convergence. Of these, for phylogenetic analysis, parallelism is the most important, since it involved development of similar but non-homologous character states in relatively closely related lineages. Hecht and Edwards (1977) correctly state that failure to recognize parallelism is probably the most common cause of misinterpretation of phylogenetic relationships. Recognition of parallelisms is discerned not only by subtle differences in development and/or structure that indicate non-homology, but also by degree of congruence of character states in a reconstructed phylogeny under the principle of parsimony. (While there is no reason to believe that evolution produces parsimonious character state distributions, rejection of parsimony as a working principle should be done only in response to strong evidence to the contrary.) Distribution of character states in a cladogram is very sensitive to hypotheses about relative weight of characters and polarity of transformation series. Character weighting is necessary because some characters have more reliable information about phylogenetic relationships than others. That is, some characters are less likely to be derived in parallel and/or parallelisms are more easily recognized in these characters than in others. Hecht and Edwards (1977) review suggestions for weighting characters by Wilson (1965), Inger (1967), Kluge and Farris (1969) and Hecht and Edwards (1976). In general, these authors agree that characters of low weight are those which involve loss or reduction of structures, those resulting from common growth processes, and those which show great variability in other groups. I would add to these, those characters for which polarity of the transformation series is not clearly analysed. Those which should be given high weight have unusual developmental patterns, are parts of integrated complexes, or are innovative and unique for the transformation series. These criteria are generally accepted in this treatment, but evaluation of each character must be done independently.

Development of hypotheses about polarity of transformation series is fundamental to character analysis. Subsequently, the literature about methods for determination of polarity is extensive. De Jong (1980) has critically reviewed the main methods for recognition of polarity and major recent discussions are found in Hecht and Edwards (1978) and Watrous and Wheeler (1981).

Generally, determination of polarity of a transformation series requires comparison of the states of the character system both among the taxa being compared (in-group comparisons) and among closely and more distantly related taxa (out-group comparison). In the simplest instance, if two states of a character occur within a taxon, and only one is found in out-group comparison, then the more restricted state is considered the apotypic condition (Watrous and Wheeler 1981). The polarized character can then be compared with others for congruence. In practice, more complex distributions of character states may make this much more difficult than this example would indicate (see de Jong 1980, Watrous and Wheeler 1981, and references included therein).

In this revision, members of the subtribe Gyrophaenina provide in-group comparisons, while members of the subtribe Bolitocharina provide out-group comparisons from a closely related group, and the aleocharines as a whole provide more distantly removed comparisons. In general, it is argued here that a character state found in the bolitocharines and some, but not all, gyrophaenines is plesiotypic.

In order to facilitate critical evaluation of the character states and hypotheses about polarity of transformation series presented here, I use the same format for discussion of each character. This includes:

1) recognized states of the character; 2) the transformation series recognized among these traits; 3) hypotheses and justification for hypotheses about plesiotypic and apotypic states; 4) specific problems associated with interpretation of individual characters plus alternative hypotheses; and 5) probable usefulness of the character in phylogenetic analysis. Character states discussed in this study are summarized in Table 1, and known distribution of these states among gyrophaenine genera is summarized in Table 2.

### 4.1.2 Character Systems: Analysis

**Character 1 – Body setae: microsetae**

States of this character among the gyrophaenines form a more or less continuous series, which is conveniently, though arbitrarily divided into 4 states: 1) setae numerous, more or less short, densely and uniformly distributed over the body ($A$); 2) setae numerous, more or less long and silky, densely and uniformly distributed ($B$); 3) setae short, number reduced, body subglabrous ($C_1$); and 4) setae short, number markedly reduced, body more or less glabrous ($C_2$). Of these, State $A$ is considered to be plesiotypic, on the basis of out-group comparison. It characterizes specimens of most bolitocharines and many other groups of aleocharines. Two transformation series of this character are recognized: one in which short, numerous setae become long, silky setae ($A \rightarrow B$); and one in which number and density of setae are reduced ($A \rightarrow C_1 \rightarrow C_2$).

Alternative hypotheses about polarity of this character are hard to justify. State $C_1$ characterizes specimens of many species of *Gyrophaena* which also have a relatively large number of plesiotypic states of other characters. This state may be hypothesized to be the plesiotypic condition. However, scarcity of this state among bolitocharines argues against this. Also, this polarity would require evolution of an increased number of setae. While possible, this hypothesis seems less parsimonious than one in which reduction was more common.

Alternatively, State *B* could be considered plesiotypic. This hypothesis is given some justification by origin near the base of the cladogram of both genera whose members have this state. Absence of this state among bolitocharines, and rarity of this condition among other aleocharines seems to argue against this.

Because the states of this character are arbitrary divisions of a continuum, it is difficult to place the condition of some specimens into one or another. Also, because one transformation series ($A \rightarrow C_1 \rightarrow C_2$) is regressive, it has almost certainly occurred many times independently. Therefore, this character is unreliable for phylogenetic inference.

### Character 2 – Body setae: macrosetae

As for Character 1, the 3 states are more or less arbitrary divisions of a continuum: 1) macrosetae small, difficult to distinguish from microsetae (*A*); 2) macrosetae larger, easily distinguished from microsetae ($B_1$), and 3) macrosetae extremely large, very conspicuous ($B_2$). Of these, State *A* is considered to be plesiotypic.

Justification for this polarization is weak. State *A* is the most common condition among bolitocharines and is also commonly found among a large number of other aleocharines. If this polarity is correct, a single transformation series of increasing size and prominence of macrosetae is produced ($A \rightarrow B_1 \rightarrow B_2$). This is probably too simple and additional study would reveal a more complex set of possible character states.

Because the states are arbitrary parts of a continuum, it is often difficult to interpret. Also, some specimens show 2 or more states of macrosetae, depending on the setae considered. In addition, apotypic states have almost certainly been derived a number of times independently within the gyrophaenines. Therefore, this character is not very useful for phylogenetic analysis.

### Character 3 – Sculpture

Three states of this character are recognized: 1) body uniformly reticulate (*A*); 2) body sculpture obsolete or smooth on one or more sclerites ($B_1$); and 3) sculpture absent, integument uniformly smooth ($B_2$). State $A$ is considered plesiotypic. Justification of this polarity is by both out-group and in-group comparison. Most bolitocharines and many other aleocharines in many groups have reticulate integumental sculpture. Also, specimens of many species in almost all genera of gyrophaenines exhibit State $A$. If this polarity is correct then a single transformation series is indicated ($A \rightarrow B_1 \rightarrow B_2$).

Reticulate integumental sculpture is a basic and very common type of sculpture among staphylinids. Independent evolution of this state, or reversion to a reticulate condition from smooth integument seems a less parsimonious hypothesis than independent loss of reticulate microsculpture in a number of lineages of gyrophaenines. However, reversion from apotypic to plesiotypic states must be considered possible. Character States $A$ and $B_2$ are precisely defined and therefore easy to interpret. However, State $B_1$ is a conglomeration of similar types of states, each of which may have been derived independently from an $A$-type ancestor or from a previous, relatively more plesiotypic $B_1$-type ancestor.

Because of the above problems, and because apotypic states are regressive, this character is not reliable for phylogenetic inference.

**Character 4 – Head: medial macrosetae**

Two states are known: 1) a pair of macrosetae medially on vertex (*A*), and 2) macrosetae absent from vertex (*B*). State *A* is considered to be plesiotypic, based solely on in-group comparison. Similar macrosetae are not known among bolitocharines, or, to my knowledge, among other aleocharines. Among gyrophaenines, there are macrosetae on the vertex in most members of *Brachida* and specimens of a very few species of *Gyrophaena* and *Eumicrota*. This distribution suggests that such macrosetae were present in ancestral gyrophaenines, and these have subsequently been lost from most lineages.

The alternative hypothesis, that macrosetae on the vertex are derived within gyrophaenines is possible. However, the uniform position of these macrosetae, and the phylogenetically disjunct distribution of such macrosetae do not support this hypothesis. The possibility that presence of macrosetae may be apotypic for the Gyrophaenina as a whole is given support by absence of such setae from out-groups. This distribution may be a result of inadequate survey of this character within these groups. Even so, the polarity of the transformation series given above (*A*→*B*) remains correct within the context of the gyrophaenines.

Because apotypic states of this character are regressive and loss of macrosetae may have occurred numerous times within the gyrophaenines, this character is of little use for phylogenetic inference.

**Character 5 - Infraorbital carina**

Two states are considered: 1) infraorbital carina well developed, complete ventrally (*A*), and 2) infraorbital carina incomplete, reduced or absent ventrally (*B*). Of these, State *A* is considered apotypic. Justification for this hypothesis is well established from both out-group and in-group comparison. An infraorbital carina is well developed among most bolitocharines, many other aleocharines and most gyrophaenines.

Because apotypic states are regressive, it has very limited use in phylogenetic inference.

**Character 6 - Head: lateral macrosetae**

Two states known: 1) macrosetae (other than a medial pair in specimens of a few species) absent from the dorsal surface of the head (*A*), and 2) two macrosetae on dorsal surface of the head on each side, medial to the anterior and posterior margin of the eye (*B*). Based on both in-group and out-group comparison, State *A* is considered plesiotypic. Macrosetae in this position are unknown among bolitocharines and most gyrophaenines. Among gyrophaenines, such macrosetae are known only in the subgenus *Acanthophaena* of *Phanerota* and are probably uniquely derived within the subgenus.

Because of the limited distribution of apotypic states of this character, it is not useful for phylogenetic inference at the generic level. However, it does provide evidence that the subgenus *Acanthophaena* is a monophyletic assemblage.

**Character 7 – Eyes**

Two states are recognized: 1) eyes moderate in size (*A*), and 2) eyes extremely large, prominent (*B*). Based on both in-group and out-group comparison, State *B* is considered apotypic. Very large eyes are not found among bolitocharines, most other aleocharines, or among most gyrophaenines. Among gyrophaenines, extremely large eyes are found among members of the genus *Phanerota* and are probably uniquely derived within that genus.

Because of the limited distribution of this character within gyrophaenines, it is not useful for intergeneric phylogenetic inference. However, it provides strong evidence that *Phanerota* is a monophyletic assemblage.

**Character 8 – Antenna: antennomere 4**

Two states are recognized: 1) antennomere 4 similar in setation and general shape to antennomeres 5-10 (*A*), and 2) antennomere 4 similar in setation and general shape to antennomeres 1-3 (*B*). Of these, State *A* is considered plesiotypic, based on out-group comparison. Most bolitocharines and many other aleocharines exhibit the plesiotypic condition.

Although in words, the states of this condition appear ambiguous, it is, in fact, within gyrophaenines, seldom difficult to assign an observed condition to one or the other states. Intermediate conditions are found only among some members of *Brachida*. Modification of antennomere 4 to a general form different from antennomeres 5-10 gives the antennae of those gyrophaenines possessing the apotypic condition a distinctive appearance.

Though conditions similar to State *B* may have evolved numerous times among other aleocharines, there seems little justification for the hypothesis that State *B* is plesiotypic among gyrophaenines.

This character seems fairly useful for phylogenetic inference within the gyrophaenines.

**Character 9 – Labrum: number of setae**

Two states are recognized: 1) labrum with numerous setae in addition to the basic setal pattern (*A*) (see Section 3.1.1.7 for description), and 2) labrum with few or no setae other than those in the basic pattern (*B*). Of these, State *A* is considered plesiotypic. Justification for this hypothesis is from both in-group and out-group comparisons. Some bolitocharines and many other aleocharines have numerous setae on the labrum. Among the gyrophaenines, State *A* is found among those groups which also exhibit other characters on the labrum believed to be plesiotypic.

It is important to note that many bolitocharines and also many other aleocharines exhibit conditions similar to State *B*. This provides some justification for the alternative hypothesis that State *B* is the plesiotypic condition. This is undeniably possible, but the association of State *A* with other presumed plesiotypic character states in the labrum of gyrophaenines, while weak evidence, is suggestive that state *A* is plesiotypic. Also, acceptance of State *B* as plesiotypic would require that apotypic states involve a gain rather than a loss. Without at least rudimentary evidence to the contrary, it seems more parsimonious to postulate a loss rather than a gain. Therefore, the hypothesis that State *A* is plesiotypic within the gyrophaenines seems to be the most parsimonious hypothesis. This implies that conditions similar to State *B* among other aleocharines are the result of independent evolution of this state, perhaps numerous times.

This character has limited use for phylogenetic inference among gyrophaenines. However, because of the relatively weak justification for character polarity and because the regressive nature of the apotypic states suggests the possibility that this state may have arisen several times independently within the gyrophaenines, this character must be used with caution.

**Character 10 – Labrum: α-sensillum**

Two states of this character are recognized: 1) α-sensillum filiform, seta-like (*A*), and 2) α-sensillum thickened, hyaline. State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Most bolitocharines, many other aleocharines and most gyrophaenines exhibit State *A*.

Apotypic states are uncommon and erraticaly distributed among several genera of gyrophaenines. The apotypic condition has probably been derived independently a number of times in one or more lineages within several genera. Therefore, this character is not useful for phylogenetic analysis at the level considered here.

**Character 11 – $\epsilon$-sensillum**

Three states are recognized: 1) $\epsilon$-sensillum large, indistinguishable from labral setae (*A*); 2) $\epsilon$-sensillum setose, but much smaller than labral setae ($B_1$); and 3) $\epsilon$-sensillum reduced to a small peg-like object ($B_2$). Of these, State *A* is considered plesiotypic, based on occurrence of State *A* in association with other plesiotypic conditions in both gyrophaenines and other aleocharines.

If this polarity is correct, then a single transformation series based on progressive reductions of the $\epsilon$-sensillum can be recognized ($A \rightarrow B_1 \rightarrow B_2$).

Justification for the hypothesis that State *A* is plesiotypic is not strong. However, the alternative hypothesis, that State $B_2$ is plesiotypic and more apotypic states of this character result in more seta-like $\epsilon$-sensilla, does not seem to be suggested by either in-group or out-group comparison.

Weak justification of polarity and the fact that apotypic states of this transformation series involve regression suggests that this character has limited value for phylogenetic inference.

**Character 12 – Labrum: position of lateral sensilla row**

Two states are recognized: 1) sensilla of row near or at lateral margin of labrum (*A*), and 2) sensilla of row more or less distant from lateral margin (*B*). Of these, State *A* is considered plesiotypic. Justification for this hypothesis is from both in-group and out-group comparison. Among gyrophaenines, State *A* occurs among species which arise early in the cladogram, and in association with other presumed plesiotypic labral conditions. State *A* is also found among many bolitocharines.

Since State *B* also occurs in other aleocharines, it is possible that this is the plesiotypic condition. However, in-group comparisons among the gyrophaenines do not support this.

Weak justification of the polarity of this transformation series suggests that the value of this character for phylogenetic inference is uncertain.

**Character 13 – Labrum: development of lateral sensilla row**

Two states are recognized: 1) 4 or 5 well developed sensilla in row (*A*), or 2) number and development of sensilla less (*B*). Based on both in-group and out-group comparison, State *A* is considered plesiotypic. State *A* is the most common condition among gyrophaenines and occurs in specimens of at least some species in all genera. Also, among gyrophaenines, State *A* occurs in all species of groups placed near the beginning of the cladogram and in association with other presumed plesiotypic states in the labrum of these species. In addition, many bolitocharines and many other aleocharines have State *A*.

The wide distribution of the plesiotypic condition among gyrophaenines makes this character of limited use for phylogenetic inference at the generic level.

**Character 14 – Labrum: position of A.L.1 and A.L.2**

Two states are recognized: 1) origin of A.L.1 and A.L.2 more or less distant from the margin of the labrum (*A*), and 2) origin of A.L.1 and A.L.2 at the margin of the labrum (*B*). State *A* is considered plesiotypic, with reservations, based on both in-group and out-group comparison. Among gyrophaenines State *A* occurs in association with other presumed plesiotypic conditions. Also, State *A* occurs in specimens of some species in most genera. In addition, most bolitocharines have State *A*. These justifications are weakened by the wide distribution of State *B* among gyrophaenines, bolitocharines and other aleocharines.

While the condition of this character in most specimens is relatively easy to assign to one or the other of these states, in specimens of some species, intermediate conditions exist (e.g. one seta of pair near and one distant from labral margin (Figures 50), which makes this character difficult to use in practice.

Weak justification for polarity of the transformation series, intermediate states, and probable multiple derivation of the presumed apotypic condition suggest that this character has little use in phylogenetic inference at the present time.

**Character 15 – Labrum: internal setose areas**

Two states are recognized: 1) densely setose area present internally on each side of labrum (*A*), and 2) densely setose area absent internally on each side of midline (*B*). The polarity of this transformation series is not clear. Presence of State *A* only among species which arise near the base of the cladogram, and association with other labral character states presumed to be plesiotypic, suggest that this state is plesiotypic among the gyrophaenines. This hypothesis is given some support by the fact that State *A* occurs in some, but not all, species in both *Probrachida* and *Brachida*. If this hypothesis is correct then State *B* would have been independently derived by species within each of these genera, and also all remaining gyrophaenines.

The alternative hypothesis, that State *B* is plesiotypic, is supported by the fact that I have not observed State *A* among the bolitocharines that I have examined, and the distribution of State *A* is unknown among other aleocharines. This suggests that State *A* may be derived within the lineages which lead to *Probrachida* and *Brachida*. Because it is not clear whether these two genera are derived from a common ancestor (see discussion in section 4.2.2.5 for details), it is uncertain whether this character must have been derived once or twice within the gyrophaenines. However, in either instance, if State *A* is a derived condition in the ancestor(s) of the two lineages of gyrophaenines in which it occurs, then other species in each lineage must have reverted to the plesiotypic condition independently.

I am unable to favor one of these two alternatives over the other. The hypothesis that State *A* is plesiotypic is the most parsimonious, but is not supported by out-group comparison. In contrast, the hypothesis that State *B* is plesiotypic is supported by limited out-group comparisons, but is less parsimonious because it requires assumption of regression to a plesiotypic state in at least some species. A more thorough study of this character within both bolitocharines and other aleocharines would probably allow one to choose between these hypotheses.

Because of the uncertainty of polarity of the transformation series of this character, it is not useful for phylogenetic inference.

**Character 16 – Mandibles: form of apex**

Three states of this character are recognized: 1) neither mandible bifid at apex (*A*); 2) left mandible bifid at apex (*B*); and 3) both mandibles bifid at apex (*C*). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. State *A* is distibuted among most gyrophaenines. State *B* is characteristic of specimens of most species of *Brachida*, while States *A*, *B* and *C* are all distributed within the genus *Probrachida*. It is not clear whether two transformation series ($A \rightarrow B$ and $A \rightarrow C$) are represented by these states, or only a single series ($A \rightarrow B \rightarrow C$). This is an important consideration, since if only one transformation series is represented, it implies the possibility of a sister group relationship between *Probrachida* and *Brachida*. If, on the other hand, two series are involved, then the evidence for a sister group relationship between members of these two genera is weaker. The problem is in presence of all three states among members of *Probrachida*. This implies either independent derivation of bifid mandibles, or reversion to a plesiotypic condition.

**Character 17 – Mandibles: internal tooth**

Three states of this character are recognized: 1) right mandible with a well developed internal tooth (*A*); 2) mandibles without an internal tooth (*B*); and 3) both mandibles with a well developed internal tooth (*C*). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Presence of an internal tooth is widely distributed among bolitocharines, other aleocharines and gyrophaenines. Two transformation series among gyrophaenines are indicated. Absence of an internal tooth on the right mandible is considered a loss (*A*→*B*), while presence of an internal tooth on the left mandible is considered a gain (*A*→*C*).

Because the first transformation series is regressive, and distribution of the second very limited, this character has limited application for phylogenetic inference among gyrophaenine genera.

**Character 18 – Lacinia: form of apex**

Two states of this character are recognized: 1) apex of lacinia more or less acute (*A*), and 2) apex of lacinia obliquely truncate (*B*). Because State *A* characterizes almost all aleocharines except gyrophaenines, this state is considered plesiotypic. All members of the subtribe Gyrophaenina have State *B* and it is considered to be uniquely derived within this group. The obliquely truncate form of the apex of the lacinia of gyrophaenines is actually one of a set of highly integrated characters which, in combination, are associated with the feeding behavior of these beetles (see section 3.1.1.9).

Since all gyrophaenines have the apotypic state for this character, it is not useful for phylogenetic inference whthin the group. However, it does provide evidence that the gyrophaenines are monophyletic.

**Character 19 - Lacinia: apical teeth**

Two states are recognized: 1) teeth on apex of lacinia relatively few, in, at most, a loosely defined patch, slightly, or not at all differentiated from the lateral teeth or spines (*A*), and 2) teeth on apex of lacinia numerous, closely spaced, in a well defined patch, well differentiated from the lateral teeth and spines (*B*). State *A* is considered plesiotypic, based on out-group comparison. All bolitocharines and many other aleocharines have State *A*. In addition, among those aleocharines for which mouthpart structure is accurately known, only gyrophaenines have State *B*.

State *B* is considered a uniquely derived condition within Gyrophaenina, and, as such, provides evidence that they form a monophyletic assemblage.

State *B* of this character is part of an integrated complex of characters including State *B* of Character system 18 (see above).

**Character 20 - Lacinia: teeth on inner face**

Three states are recognized: 1) numerous, dense, often spinelike, teeth on inner face of lacinia (*A*), and 2) few, more or less scattered, teeth on inner face of lacinia ($B_1$); and 3) inner face of lacinia without teeth ($B_2$). Of these, State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Members of *Probrachida* have

State $B_1$ of this character in association with states of other characters which are almost certainly plesiotypic in relation to the remaining gyrophaenines. All other gyrophaenines have State $B_2$ of this character. State $A$ is found among all bolitocharines and many other aleocharines.

States are apparently all part of a single transformation series ($A \rightarrow B_1 \rightarrow B_2$). Thus, State $B_1$ is intermediate between numerous teeth of bolitocharines and complete absence of teeth from all other gyrophaenines. Therefore, State $B_1$ is plesiotypic in relation to State $B_2$ within the context of the Gyrophaenina.

This character is very useful for phylogenetic inference at supergeneric levels within Gyrophaenina.

### Character 21 – Lacinia: setae on inner face

Three states are recognized: 1) setae on inner face of lacinia very numerous, densely and irregularly scattered ($A$); 2) setae less numerous, few to many, more or less loosely and irregularly scattered ($B_1$); and 3) setae on inner face of lacinia few to many, in a well differentiated vertical row ($B_2$). State $A$ is considered plesiotypic, based on both in-group and out-group comparisons. State $A$ occurs in all bolitocharines and many other aleocharines. State $B$ characterizes in specimens of a number of groups of gyrophaenines. In specimens of *Probrachida* and *Brachida*, State $B$ is found in association with other characters of the maxillae which are probably primitive. Most gyrophaenines have State $B_2$.

It seems most likely that a single transformation series is represented by the states of this character ($A \rightarrow B_1 \rightarrow B_2$). In contrast, it is possible that among the states characterizing gyrophaenines, State $B_1$ is not the direct precursor of $B_2$. However, presence of both States $A$ and $B_1$ among species of *Probrachida* and *Brachida*, and States $B_1$ and $B_2$ among species of *Agaricomorpha* and *Sternotropa* suggest that the first hypothesis ($A \rightarrow B_1 \rightarrow B_2$) is most likely correct.

Although apotypic states are apparently subject to independent derivation within the gyrophaenines, when considered with other characters, this one is useful for phylogenetic analysis.

**Character 22 – Galea: arrangement of apical setae**

Three states are recognized: 1) setae numerous, in close, numerous (8-10) rows ($A$); 2) setae numerous, rows fewer (5-8), but close ($B_1$); and 3) setae less numerous, in 4 well separated rows ($B_2$). Of these, State $A$ is plesiotypic, based on both in-group and out-group comparison. State $A$ characterizes most bolitocharines, many other aleocharines, and some members of *Brachida* among gyrophaenines. Among gyrophaenines, State $B_1$ occurs in members of both *Probrachida* and *Brachida*. All other gyrophaenines have State $B_2$.

Since, among gyrophaenines, States $A$ and $B_1$ are associated with states of other characters of the maxillae believed to be plesiotypic, and State $A$ is widely distributed in the out-group, a single transformation series is suggested ($A \to B_1 \to B_2$).

Although apotypic states are regressive, the end point of the reduction in number of rows of galeal setae is not simply a series of variously reduced states. Instead, among gyrophaenines at least, the end point of this reduction is uniformly constant in expression as 4 distinct, widely spaced rows of setae. In addition, the end point of this transformation series (State $B_2$) is found, with little modification, among members of many lineages of gyrophaenines. Therefore, although the apotypic states are regressive, the uniformity of the end of the transformation series suggests that it has been derived only once. Therefore, this character appears to be very useful for phylogenetic inference.

**Character 23 – Galea: structure of apical setae**

Two states are recognized: 1) setae on apex of galea long, filiform, setose ($A$), and 2) setae on apex of galea flattened, subspatulate or plate-like ($B$). Based on both in-group and out-group comparison, State $A$ is considered plesiotypic. State $A$ characterizes most bolitocharines and most other aleocharines. In addition, among gyrophaenines, State $A$ is found in members of *Probrachida* and in members of some species of *Brachida*. All other gyrophaenines have State *B* of this character.

Presence of both States *A* and *B* among species of *Brachida*, and State *B* among specimens of some species of bolitocharines suggest that the derived state of this character may be part of a functional complex related to fungus feeding. It could therefore have been derived any number of times independently in response to mushroom feeding. However, because of the invariance of State *B* in all gyrophaenines except *Probrachida* and *Brachida*, and uniform association of State *B* with the apotypic state of Character 22, it seems most parsimonious to consider State *B* to be of monophyletic origin in all those gyrophaenines in which it occurs except *Brachida*. This character is therefore very useful for phylogenetic inference.

### Character 24 – Labium: form of ligula

Six states are recognized: 1) ligula elongate, bifid at apex (*A*); 2) ligula short, entire, protruding and parallel sided (*B*); 3) ligula short, entire, broadly rounded (*C*); 4) ligula short, protruding, parallel sided, divided 1/2 to 2/3 distance to bases into 2 more or less sharply pointed lobes ($D_1$); 5) ligula short, protruding, parallel sided, divided almost or fully to base into 2 pointed or acutely rounded lobes ($D_2$); and 6) ligula elongate, parallel sided, anterior 1/3 divided into 2 divergent lobes (*E*). Of these, State *A* is the inferred ancestral condition for gyrophaenines. This condition of the ligula is not presently known in any gyrophaenine. It is instead inferred as ancestral because it is very similar to the condition found among bolitocharines and many other aleocharines. Condition of the ligula in bolitocharines (Figure 118) is probably similar to that of the common ancestor of the bolitocharines and gyrophaenines (based on additional out-group comparisons with the remainder of the Aleocharinae). It is, therefore, most parsimonious to hypothesize that the ancestor of the gyrophaenines possessed a ligula more similar to that of bolitocharines than to that represented in any extant gyrophaenine. No attempt has been made to arrange the other states of this character in a single transformation series (except $D_1$ and $D_2$). This is because I do not have evidence which allows defensible hypotheses about which, if any, of the known states of the ligula in gyrophaenines is plesiotypic, or even which is most similar to the type from which all known types are derived. It seems, based on simplicity of structure, that two hypotheses could be considered. First, State *C*, characteristic of members of *Probrachida*, *Brachida*, and *Encephalus*, might be plesiotypic. This is suggested by occurrence of this state among species of *Probrachida* and *Brachida* placed near the base of the cladogram and possessing a large suite of other plesiotypic character states. However, it seems difficult to imagine how States $D_1$, $D_2$ and *E* could have been derived form this character state. Alternatively, State *B*, characteristic of members of *Gyrophaena*, *Phanerota* and *Eumicrota* could be similar to the ancestral condition. It seems that a condition of the ligula similar to this could easily be modified to all conditions known within gyrophaenines. However, State *B* is limited to a single lineage. If similar to the primitive condition, it might be expected to occur in more or less unmodified form in other lineages of gyrophaenine.

In addition, both these hypotheses suffer from the facts that neither occurs among bolitocharines, and both are uncommon among other aleocharines.

It therefore seems most parsimonious to recognize the following transformation series among these character states: $A \to B$, $A \to C$, $A \to D_1 \to D_2$, $A \to E$(?). The last, $A \to E$, is very uncertain because placement of *Neobrachida*, specimens of which have State *E*, is inadequately established. Based on a tentative placement of *Neobrachida* near *Sternotropa* (see Section 4.2.2.7.4), a more reasonable transformation series would be $D_1 \to E$.

The most reasonable alternative to the series presented above would be: $A \to B$, $B \to C$, $B \to D_1 \to D_2$ (*E* as above), based on the assumption that State *B* is plesiotypic within the gyrophaenines. As noted above, this hypothesis cannot be markedly supported.

Whether one considers each of State *B* through *E* to be apotypic within the context of gyrophaenines, or whether one considers State *B* to be plesiotypic, does not affect the structure of sister group relationships in the phylogeny. However, it does affect the way that condition of the ligula as a character supports those relationships (see discussion in Section 4.2.2.8).

In spite of the problems outlined above, the fact that all of States *B* to *E* of this character are apotypic in relation to that found in the ancestor of the gyrophaenines, and that States *C* and *D* are independently derived states within the gyrophaenines, seem well supported. Therefore, with the additional reservations discussed in Section 3.1.1.10, this character is very useful for phylogenetic inference.

**Character 25 – Labium: number of medial setae**

Three states are recognized: 1) two medial setae present (*A*); 2) one medial seta present ($B_1$); and 3) medial setae absent ($B_2$). Of these states, *A* is considered plesiotypic, based on both in-group and out-group comparisons. Most bolitocharines, most aleocharines, and, among gyrophaenines, members of *Probrachida*, have two medial setae. As far as is known all other gyrophaenines have State $B_1$ except for a few members of the genera *Sternotropa*, *Gyrophaena* and *Phanerota*, which have State $B_2$.

A single transformation series of these character states is indicated ($A \rightarrow B_1 \rightarrow B_2$).

Although State $B_1$ occurs in a few bolitocharines and some other aleocharines, these conditions are probably independently derived in these groups. In addition, the invariant occurrence of State $B_1$ among all gyrophaenines except *Probrachida* (here State $B_2$ is considered a secondary modification of State $B_1$) indicates that State $B_1$ probably evolved only once (perhaps twice, depending on relationships of *Brachida*; see section 4.2.2.5) within the gyrophaenines.

Therefore this character is useful for phylogenetic analysis.

**Character 26 – Pronotum: sinuosity of the base**

States of this character among gyrophaenines are arranged in a continuously varying transformation series. However, this series is conveniently, although arbitrarily, divided into 3 character states: 1) hind margin of pronotum markedly bisinuate (*A*); 2) hind margin of pronotum slightly bisinuate ($B_1$); and 3) hind margin of pronotum not bisinuate ($B_2$). Based on both in-group and out-group comparisons, State *A* is considered plesiotypic. A markedly bisinuate hind margin of the pronotum (State *A*) is rather widely distributed in many groups of gyrophaenines. Reduction of bisinuations to a smoothly rounded hind margin appears to be most commonly associated with subsequent narrowing of the pronotum, an apotypic character state (see Character 28). In addition, State *A* is widely distributed within the Aleocharinae. Bolitocharines, however, do not have a bisinuate hind margin of the pronotum. Under this interpretation, State $B_2$ in bolitocharines is derived independently from State $B_2$ in gyrophaenines. A single transformation series is indicated ($A \rightarrow B_1 \rightarrow B_2$). Because the states are arbitrary divisions of a continuum, and because of the probably multiple derivation of apotypic states within gyrophaenines, this character has very limited use for phylogenetic inference.

### Character 27 – Pronotum: median emargination of base

Two states are recognized: 1) hind margin of pronotum without a medial emargination (*A*), and 2) hind margin of pronotum with a broad to more or less acute medial emargination (*B*). State *A* is considered plesiotypic. It is the condition among most gyrophaenines, all bolitocharines, and most other aleocharines.

State *B* is uncommon among gyrophaenines and distributed in groups which are phylogenetically widely separated. It has probably been derived a number of times independently. Therefore, this character is not very useful for phylogenetic analysis.

### Character 28 – Pronotum: shape

Three states are recognized: 1) pronotum more or less markedly transverse (*A*); 2) pronotum more or less broadly oval ($B_1$); and 3) pronotum more or less subquadrate ($B_2$). Of these, State *A* is considered plesiotypic, based primarily on in-group comparisons. State *A* is characterizes members of a number of genera of aleocharines. However, all bolitocharines that I have examined have States $B_1$ and $B_2$.

Occurrence of State *A* among a number of different groups of gyrophaenines, usually in association with states of other pronotal characters believed to be plesiotypic, suggests that this state is plesiotypic within the Gyrophaenina.

Because of the probable multiple origin of apotypic states among gyrophaenines, this character has limited use for phylogenetic inference.

**Character 29 – Pronotum: flexion of lateral border**

Degree of ventral flexion of lateral borders of the pronotum among gyrophaenines is arranged in a continuum, from extremely deflexed to not deflexed. This continuum is conveniently, though arbitrarily, divided into 3 states: 1) lateral borders of pronotum moderately to slightly deflexed (*A*); 2) lateral borders of pronotum not at all or very slightly deflexed (*B*); and 3) lateral borders of pronotum very markedly deflexed (*C*). Of these State *A* is considered plesiotypic base on both in-group and out-group comparisons. Many aleocharines have a moderately convex pronotum. This prompted Seevers (1978) to suggest that the generalized condition of the aleocharine pronotum was rather convex, and flattening of the pronotum is derived. However, most bolitocharines have State *B* of this character. State *A* is widely distributed among gyrophaenines and occurs in at least some members of almost all genera. State *B* appears to have been derived several times independently: however, among gyrophaenines, very markedly flattened pronota only occur among species of *Gyrophaena* and *Phanerota*.

Very markedly convex pronotun (State *C*) is also considered derived (modified from State *A*). This condition is limited among gyrophaenines to members of *Brachychara*, *Adelarthra* and *Encephalus*.

Therefore, two transformation series are suggested in this character (*A*→*B* and *A*→*C*).

Ambiguity of assigning conditions observed in specimens, and probable multiple origin of derived states among gyrophaenines make this character of very limited value for phylogenetic inference.

**Character 30 – Hypomera: visibility**

Expression of this character is correlated with expression of Character 29 as discussed in Section 3.1.1.11. As in Character 29, the states are arranged in a continuum, arbitrarily divided into three states: 1) hypomera almost invisible in lateral view (*A*); 2) hypomera narrowly visible in lateral view ($B_1$); and 3) hypomera broadly or in large part visible in lateral view ($B_2$). State *A* is considered plesiotypic, Justification for this hypothesis is very similar to that presented for polarity of Character 29. Invisibility of the hypomera in latral view is probably plesiotypic for aleocharines as a group (Seevers, 1978), and State *A* is widely distributed among aleocharines and gyrophaenines. However, as far as is known, all bolitocharines have States $B_1$ or $B_2$ of this system. Under the hypothesis presented above, apotypic states among bolitocharines are derived independently of similar apotypic states in gyrophaenines. Among gyrophaenines, apotypic states, and particularily State $B_2$, are widely distributed only in the genera *Gyrophaena*, *Phanerota* and a few species of *Eumicrota*. However, usefulness of this character for phylogenetic inference is somewhat limited by the presence of all three character states (*A*, $B_1$, $B_2$) within *Gyrophaena*. Some examples of State *A* within *Gyrophaena* may be secondary derivation of this condition from a more apotypic state. However, among some groups (e.g. *Gyrophaena hubbardi* Seevers and related species) State *A* of this character is associated with other presumed plesiotypic states of prontal characters.

**Character 31 – Scutellum: visibility**

Two states are recognized: 1) scutellum visible in dorsal view (*A*), and 2) scutellum hidden by the base of the pronotum in dorsal view (*B*). Based on in-group and out-group comparisons, State *A* is considered plesiotypic for gyrophaenines. Most aleocharines, all bolitocharines I have examined, and most gyrophaenines have State *A*.

The limited distribution of apotypic states makes it of relatively little use in phylogenetic inference at the genus level.

**Character 32 – Elytron: latero-apical angle**

States of this character are arbitrary and rather ambiguous, but convenient, divisions of a continuous transformation series. These states are: 1) latero-apical angle of elytron markedly or deeply sinuate (*A*); 2) latero-apical angle of elytron weaky or shallowly sinuate ($B_1$); and 3) latero-apical angle of elytron not sinuate ($B_2$). State *A* is considered plesiotypic, based primarily on out-group comparison. A great many aleocharines in a diversity of groups and all bolitocharines have State *A*. Hammond (1975) treated sinuate latero-apical angle of elytra as a uniquely derived character within the aleocharines in relation to the sister group (within which he included the Phloeocharinae, Tachyporinae, Trichophylinae and Habrocerinae). If Hammond is correct, then sinuate latero-apical elytral angles are plesiotypic for Aleocharinae. This is the interpretation accepted in this study.

If this hypothesis is correct, then a single transformation series is indicated based on progressive loss of sinuation of the latero-apical angles ($A \rightarrow B_1 \rightarrow B_2$).

Because the apotypic states are regressive, they probably have been derived a number of times independently within Gyrophaenina. This character therefore, is not very reliable for phylogenetic inference within the gyrophaenines.

**Character 33 – Prosternum: shape**

Two more or less ambiguous states are recognized: 1) prosternum markedly transverse (*A*), and 2) prosternum slightly to moderately transverse (*B*). State *A* is considered plesiotypic. This polarity is justified primarily by in-group comparisons, and is based mainly on correlation between the states and Character 28. As discussed in Section 3.1.1.13 a transverse prosternum characterizes most specimens with markedly transverse pronota. If the hypothesis that the latter state is plesiotypic in gyrophaenines, then it follows that a markedly transverse prosternum, which is correlated with this condition, is also plesiotypic.

While this justification of this character polarity *A*→*B* is very weak, it is difficult to defend alternative hypotheses at this time. The alternative hypothesis that State *B* is plesiotypic is given some support by presence of this state in many bolitocharines. However, as noted in the discussion of Character 28, bolitocharines also have slightly transverse to subquadrate pronota, a presumed apotypic condition.

Because of the weak justification for polarity of this character, it has very limited use in phylogenetic inference.

**Character 34 – Prosternum: medial ornamentation**

Four states are recognized: 1) prosternum with a tooth, carina or knob medially (*A*); 2) prosternum with tooth, carina or knob reduced or absent (*B*); 3) prosternum with a transverse carina ($C_1$); and 4) prosternum without a transverse carina ($C_2$). State *A* is considered plesiotypic, Justified primarily on the basis of out-group comparisons. This state is widespread among aleocharines and characterizes all bolitocharines. Among gyrophaenines, apotypic states are limited to members of the "Gyrophaena" lineage (see Section 4.2.2.8) and *Probrachida* and *Brachida*, and is probably derived independently in each of these lineages. State *B* is not known among gyrophaenines, but is an inferred condition which seems to be required if the above hypothesis is correct. (It is possible, however, that the condition in members of the "Brachida" lineage represents State *B* instead of State $C_2$. If so, it is indistinguishable from State $C_2$ found in some species of *Gyrophaena* and *Phanerota*.) State *C* does not seem directly derivable from State *A* without previous reduction of the medial ornamentation.

If the above hypothesis is correct a single transformation series is indicated in which the medial ornamentation of the prosternum is reduced or lost, followed subsequently by development of a transverse carina on the prosternum. Finally, transverse carina is lost in some species ($A \rightarrow B \rightarrow C_1 \rightarrow C_2$).

This character has limited use for phylogenetic inference, and must be used with caution because two independently derived conditions (*B* and $C_2$) may be indistinguishable, and also because some apotypic states are regressive.

**Character 35 – Mesosternum: development of carina**

Four states are recognized: 1) mesosternum with a well developed median longitudinal carina from anterior margin to apex of mesosternal process (*A*); 2) medial longitudinal carina more or less reduced, not complete to end of mesosternal process (*B*); 3) medial longitudinal carina modified to a low, diffuse, broad ridge (*C*); and 4) medial longitudinal carina absent (*D*). Based on both in-group and out-group comparisons, State *A* is considered plesiotypic. The presence of a median longitudinal carina on the mesosternum is widespread among the aleocharines. It is present in all bolitocharines that I have examined, though in this group there has been secondary modification to State *B* in many species. These facts, in addition to the presence of State *A* in a number of genera of gyrophaenines, provide strong support for the hypothesis that State *A* was the condition found in the ancestor of the gyrophaenines.

Because all apotypic states are regressive, a number of different, morphologically indistinguishable transformation series are possible based on the above states. These are: 1) reduction of the posterior carina (*A*→*B*); 2) modification of the carina to a low, diffuse ridge (may be derived from either State *A* or *B*) (*A*→*C*; *B*→*C*); and 3) complete loss of the median longitudinal carina, derived from any other state (*A*→*D*; *B*→*D*; *C*→*D*).

Because apotypic states are regressive, it must be used with caution in phylogenetic inference within the gyrophaenines.

**Character 36 – Intercoxal processes: relative length**

Two states are considered: 1) mesosternal process extended to middle or slightly posterior to middle of middle coxae (*A*), and 2) mesosternal process extended to or almost extended to posterior margin of mesocoxal cavities (*B*). These character states are rather ambiguous, and intermediates between these states make this character rather difficult to use.

State *A* is probably most similar to the plesiotypic condition for gyrophaenines, based primarily on out-group comparisons. State *A* is the condition in most bolitocharines, and is widely scattered among gyrophaenines. However, variation in this system is inadequately understood. Intermediate conditions between these two states makes interpretation difficult. It seems likely that apotypic states have been derived a number of times independently. Therefore, this character should be used with caution for phylogenetic inference.

**Character 37 – Intercoxal processes: separation**

Two states are recognized: 1) mesosternal and metasternal processes more or less separated, isthmus present (*A*), and 2) mesosternal and metasternal processes more or less contiguous, isthmus absent (*B*). Based primarily on out-group comparisons, State *A* is considered plesiotypic. It is the condition of most bolitocharines and many other aleocharines. State *B* characterizes all gyrophaenines except specimens of *Agaricochara* which have a very short isthmus. Continuous middle coxae are so invariable within Gyrophaenina that it suggests that separated intercoxal processes in *Agaricochara* species may be secondary.

State *B* in specimens of a few species of bolitocharines, and some other aleocharines, are almost certainly examples of independent evolution of this condition in these groups.

Because of uniform distribution of the plesiotypic state of this character among gyrophaenines, this is not useful for phylogenetic inference within this subtribe. It does provide additional evidence that gyrophaenines are monophyletic. However, presence of State *A* in specimens of *Agaricochara* is anomalous within this hypothesis.

**Character 38 – Intercoxal processes: condition of juncture**

Two states are considered: 1) junction between mesosternal and metasternal process truncate or broadly rounded, with a distinct suture (*A*), and 2) junction between intercoxal processes fused, suture invisible (*B*). State *A* is considered plesiotypic, based on both in-group and out-group comparisons. Completely fused mesosternal and metasternal processes were not present among the bolitocharines I examined, and they are not common among other aleocharines. State *A* characterizes most gyrophaenines. From this condition, State *B* has apparently been derived independently a number of times (often within a single genus).

Because of the probable multiple origin of the apotypic condition, this character is of very limited use for phylogenetic inference.

**Character 39 – Metepisternal setae**

Four states are recognized: 1) setae on metepisternum numerous, uniformly and irregularly distributed (*A*); 2) setae on metepisternum in 2 irregular rows ($B_1$); 3) setae on metepisternum in a single well differentiated row ($B_2$); and 4) setae on metepisternum absent or very few scattered setae restricted to posterior third or less (*C*). Justification considering State *A* plesiotypic is available from both in-group and out-group comparisons. This state characterizes most bolitocharines and many other aleocharines, but among gyrophaenines is represented only in specimens of some species of *Probrachida* and *Brachida*. These groups arise near the base of the cladogram and have a number of other plesiotypic character states.

States of this character are arranged in several transformation series. The first involves progressive loss of setae of the metepisternum by reduction of the number of rows of setae ($A \rightarrow B_1 \rightarrow B_2$). The second series involves complete loss of the setae on the metepisternum. However, this condition could conceivably be derived from any of the other states ($A \rightarrow C$; $B_1 \rightarrow C$; $B_2 \rightarrow C$). At present it is impossible to distinguish between the end results of these transformation series.

Since the apotypic states involve regression, the character must be used with caution. However, as a comparative character, it is very useful for analysis of some lineages.

### Character 40 – Metepisternum: carina

Two states are recognized: 1) setose area on metepisternum not delimited anteriorly and ventrally by a carina (*A*), and 2) setose area on metepisternum delimited anteriorly and ventrally by a weak to moderately developed carina (*B*). Based on both in-group and out-group comparison, State *A* is considered plesiotypic. It characterizes most bolitocharines, and is widely distributed among other aleocharines. Among gyrophaenines, State *A* characterizes members of most genera.

State *B* has been independently derived in a few bolitocharines and several other aleocharine lineages, suggesting that the apotypic state may also be of multiple origin within Gyrophaenina. The condition of the metepisternum of most species of the "Probrachida" lineage may be confusing. In these specimens, the setose area of the metepisternum is depressed so that the setae are in a well defined groove. However, the anterior and ventral edges of this groove do not appear to be homologous to the carina located in this position in other gyrophaenines.

A problem in using this character is interpretation of the condition. The carina may be very faint and present only anteriorly, or it may be quite distinct and form a complete anterior and ventral boundary for the setose area. Intermediates between the conditions also occur. I have considered all these carinate conditions equivalent under State *B*.

This character is useful for phylogenetic inference. However, because of the possibility of multiple origin of the derived conditions, it must be used with caution.

### Character 40 – Abdomen: number of terga transversely impressed

Three states are considered here: 1) terga 3-6 moderately markedly transversely impressed (*A*); 2) terga slightly impressed, one or more of 3-5 without impressions

($B_1$); and 3) all terga without transverse impressions ($B_2$). Of these, State *A* is considered plesiotypic. Justification for this hypothesis is from both in-group and out-group comparisons. State *A* is found in all bolitocharines and in most other aleocharines. In addition, State *A* is the condition in most gyrophaenines and is found in specimens of almost all lineages.

A single transformation series is indicated for the states based on progressive loss of transverse impressions on the abdominal tergites ($A \rightarrow B_1 \rightarrow B_2$).

Difficulty in interpreting the conditions of this character is possible.

Because apotypic states are regessive, the probability of multiple origin of States $B_1$ and $B_2$ is very high. Therefore, this character has very limited value in phylogenetic inference within the gyrophaenines.

**Character 42 – Tergum 10: shape of medial setose area**

Five states are considered: 1) medial setose area of tergum 10 more or less quadrate with numerous setae (*A*); 2) medial setose area on tergum 10 more or less quadrate with fewer more widely scattered setae (*B*); 3) medial setose area on tergum 10 chevron-shaped (inverted V-shaped, point directed anteriorly) with numerous setae not in distinct rows ($C_1$); 4) medial setose area on tergum 10 chevron-shaped, setae few, in 1 or 2 (in some specimens, slightly a third) well developed rows ($C_2$); and 5) medial setose area on tergum 10 V-shaped (point of "V" directed posteriorly), setae few, in 1 or 2 distinct rows. (*D*). Based on both in-group and out-group comparisons, State *A* is hypothesized to be plesiotypic. It is widespread among aleocharines and is found among specimens of phylogenetically widely separated groups of gyrophaenines. In addition, State *A* is the condition from which all other conditions of this character could most easily be derived within gyrophaenines.

The alternate hypothesis, that State $C_1$ is plesiotypic, is given some support by the fact that this state characterizes bolitocharines. It is also the condition in many other groups of aleocharines, particularly some Oxypodini. However, it seems most parsimonious to conclude that the structurally less complex subquadrate setal patch is the true plesiotypic condition for the aleocharines as a whole. If so, then State $C_1$ has been independently evolved in bolitocharines, many groups of aleocharines, and some gyrophaenines.

If this hypothesis is correct, then at least three transformation series are indicated. The first is simple reduction in number and density of the setae ($A \to B$). The second series involves loss of setae posteriorly and medially, giving an emarginate setose area, with the trend continued to produce a chevron-shaped setose area composed of well developed rows of setae ($A \to C_1 \to C_2$). A third series involves loss of antero-medial and postero-lateral setae producing a V-shaped setose area ($A \to D$). Presumably the second and third of these series could involve State *B* as an intermediate condition.

Although the apotypic states are regressive, the patterns of loss are not uniform in the different transformation series. Therefore, though it seems likely that States $C_1$ and $C_2$ have been independently derived several times in the gyrophaenines (see Section 5.3.1.2), this character, when used with caution, is very useful for phylogenetic inference.

**Character 43 – Tergum 10: structure of medial setae**

Three states are recognized: 1) setae on tergum 10 more or less long, setiform, unmodified (*A*); 2) setae on tergum 10 more or less short and stubby, setiform ($B_1$); 3) setae on tergum 10 flattened, more or less subspatulate ($B_2$). Justification for considering State *A* plesiotypic comes from in-group and out-group comparisons. This is the condition of bolitocharines and most other aleocharines. State *A* also occurs in phylogenetically diverse groups of gyrophaenines.

If the hypothesis about character state polarity is correct, either one or two transformation series are possible based on these character states. It seems most likely that State $B_1$ is derived from State *A*. However, State $B_2$ may be derived from either State *A* or $B_1$ ($A \rightarrow B_2$; $A \rightarrow B_1 \rightarrow B_2$). It is not possible to distinguish between the end products of these two transformation series at this time.

Although multiple origin of apotypic states is possible within the gyrophaenines, the system is useful in phylogenetic inference within the group, especially when used in correlation with other characters.

**Character 44 – Spermatheca: latero-apical plate**

Two states are considered here: 1) latero-apical plate absent (*A*), and 2) latero-apical plate present (*B*). State *A* is almost certainly plesiotypic, based on out-group comparison. Although the structure of the spermatheca of aleocharines has not been studied in detail, and spermathecal structure of many groups is unknown, a latero-apical plate is known only among members of the Gyrophaenina. In addition, females of all gyrophaenines, except for a few species of *Probrachida*, have such a plate. Members of those few species of *Probrachida* which lack this plate are most parsimoniously considered to have lost this structure, since it occurs in females of closely related species. The latero-apical plate (State *B*), is, therefore, almost certainly a uniquely derived characteristic within the subtribe Gyrophaenina.

Since females of all gyrophaenines possess State *B* of this character, it is not useful for phylogenetic inference this subtribe. However, this character is of great value in supporting the hypothesis that gyrophaenines are monophyletic.

**Character 45 – Spermatheca: modifications**

Three states are considered: 1) spermatheca simple, without elongate neck (*A*); 2) spermatheca with neck elongate distal to the latero-apical plate, neck often twisted or convolute (*B*); 3) spermatheca with neck elongate proximal to the latero-apical plate, neck often twisted or convoluted (*C*). Based primarily on in-group comparisons, State *A* is considered plesiotypic. It characterizes females of a number of lineages of gyrophaenines. States *B* and *C* are limited to single lineages, and it is most parsimonious to consider them independently derived.

This character has limited use for phylogenetic inference within the gyrophaenines. It is most useful in supporting hypotheses about the monophyly of those groups within the tribe which have the derived states.

**Character 46 – Median lobe of the aedeagus**

For simplicity, only two states are considered. However, a large number of relatively plesiotypic and apotypic states can be recognized among gyrophaenine aedeagi. Outgroup comparison with bolitocharines and other aleocharine groups suggests that in the relatively plesiotypic condition, the median lobe of gyrophaenines has a simple, lobe-like apical process and a relatively short, unsclerotized, tube-like flagellum (State *A*). Relatively apotypic conditions of the median lobe include modification of the apical process to very slender, blade-like or highly complex structures, and modification of the flagellum to very slender, elongate, whip-like structures, or highly complex and more or less sclerotized structure (State *B*). Therefore, for this character, plesiotypic and apotypic conditions discussed in cladistic analysis are not specific conditions, but rather conditions relative to that hypothesized to have been present in the common ancestor of two lineages.

Because general form of the median lobe is relatively uniform within a group, this is a very useful character for phylogenetic analysis. This character can be broken down into a number of more specific systems for use at other levels of analysis.

**Character 47 – Parameres**

Justification for this character is similar to that of Character 46. Only two states are considered. In-group and out-group comparisons with bolitocharines and other aleocharines suggests that in the plesiotypic condition, the apical lobe of the paramerite of gyrophaenine parameres is symetrical, relatively simple, elongate, and with four more or less equal setae located near apex (State *A*). Relatively apotypic conditions of the parameres include modifications of the apical lobes to be asymmetrical, or very elongate, with setae very unequal in size and not all located near apex (State *B*). The specific condition considered apotypic is discussed in the appropriate section of the cladistic analysis.

Because relatively apotypic conditions are uniform in some groups, this is a useful character for phylogenetic analysis. This character can also be resolved to a number of more specific characters useful at other levels of analysis.

## 4.2 Phylogenetic Analysis

### 4.2.1 Theoretical Considerations

I agree with Whitehead (1972) and Hammond (1975) that it is important to clearly present the theoretical, philosophical and methodological basis for an analysis. Without such a clear exposition of approach, subsequent critical evaluation is difficult or ineffective. In this section, I will present a brief review of the fundamental assumptions on which the following analysis is based.

The procedure used in this treatment for reconstructing the phylogenetic relationships of groups of gyrophaenines was originally developed by Hennig (1965, 1966). Since these first expositions on phylogenetic systematics (which will be referred to here as "cladistic analysis" or "cladism") the literature on cladistic methods, philosophy, and theoretical implications has become extensive. In addition, as Bonde (1977) and Gaffney (1979) have pointed out, the ideas and methods currently considered as parts of cladistic analysis are very diverse.

Major papers which have developed cladistic methods or theory, in addition to primary papers by Hennig (1965, 1966), include Brundin (1966, 1972), Cracraft (1974), Griffiths (1974), Hecht and Edwards (1977), Nelson (1972, 1973), Platnick (1977), Schaeffer, Hecht and Eldredge (1972), and Wiley (1975). Important papers concerned with philosophical aspects of systematics include Cracraft (1978), Hull (1970, 1974, 1979), Platnick (1979), and Platnick and Gaffney (1977, 1978). Major criticisms of cladistic methods have come from Ashlock (1974), Bock (1968), Darlington (1970), Mayr (1974) and Simpson (1975).

Three recent books (Eldredge and Cracraft 1980; Nelson and Platnick 1980; Wiley 1981), while different in intent and approach, provide insight into contemporary concepts of phylogenetic inference.

I agree with Eldredge and Cracraft (1980) that reconstruction of the phylogenetic history of a group should be done using a method which is hypothetico-deductive in structure. That is, hypotheses about phylogenetic history must be presented in such a way that they can be critically evaluated, and, if inconsistant with additional evidence, be rejected. I believe that cladistic analysis is the presently available method most consistant with this requirement.

I accept the following methodological principles in relation to cladistic analysis: 1) monophyletic groups can be recognized only on the basis of uniquely shared, derived character states (autapotypy); 2) the sequence of cladistic events can be reconstructed by arranging monophyletic terminal taxa into more comprehensive monophyletic groups based on shared characters which are uniquely derived at the given level of analysis; 3) the sequence of cladogenetic events in a lineage is best expressed by a dichotomous branching diagram or cladogram, though this may not be the most exact representation of the evolutionary history of the group.

It has been clear to most taxonomists for some time that grouping of organisms based on shared homologous structures are most useful. The major contribution of Hennig (1966) was recognition that there were two levels of homology. There are those homologous structures which are uniquely shared by all members of a taxon, and assumed to have been first derived in the most recent common ancestor of that taxon (apotypies); and there are homologous structures which are shared among members of a more inclusive taxon (plesiomorphies). De Jong (1980) pointed out that most authors who have used these terms have not been very precise and have often used them as synonyms. In this treatment, I have accepted de Jong's use of the terms synapotypy and autapotypy. Synapotypy is used to denote common possession of a derived condition whether it is of monophyletic or polyphyletic origin. Autapotypy is resticted to common possession of a derived character state of monophyletic origin.

Dichotomous cleavage of lineages is accepted here as a methodological principle. For species-level taxa, this is certainly an over-simplification, and is unlikely to accurately represent evolutionary events. However, a cladogram (*sensu* Hennig 1966) is only intended to represent recency of common ancestry as indicated by distribution of shared derived characteristics. Accurate representation of evolutionary patterns such as ancestry and descent or more complex cleavages of ancestral species are matters for subsequent analysis (Eldredge and Cracraft 1980).

Higher level taxa do not evolve by cleavage of ancestral species in the same sense that species do. If higher level taxa are required to be monophyletic in a strict sense (*sensu* Hennig 1966) rather than in the sense of Simpson (1953), a dichotomous branching diagram should in principle accurately reflect both nearest common ancestor and branching sequence. In practice, though, this sequence may be very difficult to resolve. This is not true, however, if higher taxa are considered monophyletic in the sense of Simpson (1953) or if they are allowed to be paraphyletic. In the first instance (strict monophyly) ancestor-descendent relationships between higher taxa are meaningless since this would require that some of these taxa be paraphyletic, a situation not allowed by definition. In the second instance (monophyly *sensu* Simpson), ancestor-descendent relationships between higher taxa are meaningful.

This distinction is important since this revision is a treatment of higher level taxa. I have here accepted a strict definition of monophyly for higher level taxa.

### 4.2.2 Cladistic Relationships

#### 4.2.2.1 Introduction

For convenience of discussion I designate informal names for the three major lineages of gyrophaenines: the "Brachida" lineage, the "Sternotropa" lineage, and the "Gyrophaena" lineage. The "Brachida" lineage includes 2 genera: *Probrachida* n.gen., and *Brachida*; the "Sternotropa" lineage, 7 genera: *Sternotropa*, *Pseudoligota*, *Adelarthra*, *Agaricomorpha* n.gen., *Brachycara*, *Neobrachida*, and tentatively *Agaricochara*; and the "Gyrophaena" lineage, 3 genera: *Gyrophaena*, *Phanerota* and *Eumicrota*. For reasons given below, *Encephalus* is of uncertain placement and therefore not included in these informal groups.

Relationships of several genera are uncertain. The genera *Brachida*, *Adelarthra* and *Agaricochara* can be placed in several positions within the cladogram, depending on assumptions made about number and types of parallel character state evolution within related lineages. Therefore, a series of alternative hypotheses about cladistic relationships of each of these genera is provided; each hypothesis is discussed and evaluated, and, where possible, the most parsimonious, based on available data, is chosen.

Relationships of two genera, *Neobrachida* and *Encephalus* are so unclear that they cannot be placed on the cladogram with confidence. Possiblities are discussed and problems in placing them phylogenetically are outlined. However, *Neobrachida* and *Encephalus* are not included in the cladogram in Figure 260.

### 4.2.2.2 Relationships of the Subtribe Gyrophaenina within the Aleocharinae

Detailed discussion of the relationships of gyrophaenines within the Aleocharinae is seriously compromised by incomplete and inadequate knowledge of structural, behavioral and ecological diversity of this subfamily. Within the context of the present study, little can be done to remedy this situation. Detailed surveys of structural characters, particularly of mouthparts, of representatives of most major tribes and subtribes of aleocharines were undertaken. However, the large number of valid higher taxa of aleocharines and great structural diversity among them requires that such a survey must be quite superficial.

Several recent studies of groups within the Aleocharinae have provided additional background information about structural diversity, and I have relied rather heavily on these. These include Hammond (1975), Sawada (1970, 1972), Klimaszewski (1979), and Seevers (1978).

The subtribe Gyrophaenina is placed in the tribe Bolitocharini by most authors. (For a historical survey of classification of gyrophaenines, see Section 3.3.1.3). Traditionally, the tribe Bolitocharini has been comprised of those aleocharines with a 4-4-5 tarsal formula. As such, the tribe was very heterogenous and probably polyphyletic. Seevers (1978) removed several groups of aleocharines with specialized habits from the Bolitocharini and placed these in separate tribes.

While recognizing that the tribe Bolitocharini will almost certainly require additions or deletions as the aleocharines become better known, I regard Seevers' (1978) as the best available working concept of the tribe. Therefore, future reference to the tribe Bolitocharini will be the Bolitocharini *sensu* Seevers (1978). Among the aleocharines which Seevers retained in the Bolitocharini, he recognized 6 "groups", which appear equivalent to the subtribe category as used in this study. Members of the Bolitocharini are all either inhabitants of fresh mushrooms, or subcortical. Although the group still remains rather heterogenous, gyrophaenines share a number of characteristics with other members of the tribe. These include: 1) the 4-4-5 tarsal formula; 2) small rows of minute denticles or teeth on the molar region of the mandibles; and 3) similarities in the median lobe of the aedeagus (Seevers 1978). In addition to these characteristics mentioned by Seevers, all members of the tribe Bolitocharini (except gyrophaenines, the maxillae of which are probably derived from similar structures) have a similar form of the maxilla. General characteristics of the bolitocharine maxilla are shown in Figures 96, 97 and 238. All bolitocharines have a lacinia with an acute tip, a short distal comb of more or less loosely scattered teeth, a subapical broadly protruded area densely covered with spines, teeth and setae, more scattered spines and teeth proximally along inner face, and entire inner face more or less densely covered with long scattered setae. Obviously, if the maxillae of gyrophaenines are derived from structures similar to these, the amount of modification required is extensive.

Although these similarities in structure are found among members of the Bolitocharini, which of these characteristics are actually synapotypies is unknown. All share the 4-4-5 tarsal formula. However, given Seevers' interpretation of the tribe Bolitocharini, a number of other tribes share this character. The 4-4-5 tarsal formula may be a synapotypy linking supratribal taxa. If so, it will be difficult to distinguish from parallel development of similar conditions.

The denticle on the molar surface of the mandibles is a more promising character. Mandibles of all bolitocharines that I have examined have denticles. Furthermore, they are lacking from most other aleocharines including members of tribes sharing the 4-4-5 tarsal formula with bolitocharines.

Seevers (1978) suggested that these denticles on the mandibles may be associated with feeding on spores and hyphae of fungi. However, it is important to note that such denticles are not limited to bolitocharines. Seevers (1978) also reported similar denticles on the molar surface of members of the tribe Philotermitini, all of which are termitophilous. It is possible that this condition of the mandibles is independently derived in the philotermitines. However, this must be demonstrated, not assumed. In addition, a more complete survey of the mouthparts of aleocharines may show such mandibular denticles to be more widespread. No decision can be made about value of this character as a synapotypy for the Bolitocharini at the present time.

Usefulness of similarities in aedeagal structure in indicating the monophyletic nature of the Bolitocharini is uncertain. Seevers (1978) described the median lobe of bolitocharines as having a "difficult to define bolitocharine characteristic" (p.161). Such ambiguity seems to indicate that one is dealing with an impression of general similarity rather than specific aedeagal characteristics. There are, however, a suite of characteristics in which the aedeagi of members of the Bolitocharini are more similar to each other than to most other aleocharines. The aedeagus of most members of the tribe Bolitocharini has a relatively simple median lobe with a oval, rather elongate, depressor plate; a large, more or less tubular flagellum which is slightly to moderately sclerotized in many; and an ejaculatory duct which extends the entire length of the flagellum, with the opening of the duct near the apex of the flagellum. In addition, the median lobe of most bolitocharines lacks complex internal structure and extensive eversible membranes armed with hooks and spines, as commonly found among aleocharines, and many of the aedeagal specializations found in other groups, such as the "athetine bridge" (Seevers, 1978) and the deep ventro-lateral incision of the basal bulb of the aedeagus. It is by no means clear which, if any, of these similarities in the median lobe of members of the Bolitocharini are true synapotypies. It is also important to note that if these similarities are part of the "ground plan" of the bolitocharine aedeagus, then modifications of this basic type has been extensive in some groups. Also, the characteristics mentioned above as shared among the bolitocharines may also be found in different combinations in other groups of aleocharines. Much more comparative study must be done on the detailed structure of the aedeagus of aleocharines before this group of characters can be evaluated.

The gyrophaenines do not share similarities in maxillary structure with other bolitocharines. For reasons discussed more fully below, it is here predicted that the highly specialized type of maxilla of gyrophaenines is derived from a type similar to that found among other bolitocharines.

In conclusion, it is apparent that the subtribe Gyrophaenina cannot be placed within the tribe Bolitocharini based on clearly polarized synapotypies. This, however, is a result of lack of knowledge of apotypic and plesiotypic states within the aleocharines rather than an inherent ambiguity in affinities of gyrophaenines. For the present, at least, affinities of any group of aleocharine must be based on "similarity" although it is quite possible to hypothesize apotypic conditions for the highly specialized states of structures or habits found in some groups of aleocharines. The gyrophaenines share more similarities with members of the tribe Bolitocharini than with any other group. Some of these similarities may be true synapotypies, but this hypothesis must await further study. In addition, the gyrophaenines, though highly specialized themselves, lack many of the specializations of other groups of aleocharines. For example, at present, it would be difficult to justify a hypothesis that members of the tribes Aleocharini, Falagrini, or Athetini share a most recent common ancestor with gyrophaenines.

A hypothesis which must be considered is that gyrophaenines form the sister group to the entire tribe Bolitocharini, rather than being included within it. The gyrophaenines are certainly highly autapotypic in some characters in relation to other members of the Bolitocharini. However, the remainder of the Bolitocharini as a group do not seem to have autapotypies not found in gyrophaenines. Elevation of gyrophaenines to tribal rank because of their highly specialized habits would make the Bolitocharini paraphyletic. While paraphyletic groups can be justified, I will argue below that some evidence suggests that gyrophaenines share their closest common ancestor with members of a subtribe within the Bolitocharini. This relationship is best emphasized by ranking the gyrophaenines as the subtribe Gyrophaenina within the tribe Bolitocharini.

#### 4.2.2.3 The Subtribes Bolitocharina and Gyrophaenina as Sister Groups

The subtribe Bolitocharina as considered here is essentially equivalent to the group "Bolitocharae" of Seevers (1978). I differ with his interpretation of the subtribe in that I question whether *Leptusa* Kraatz should be included. All members of *Leptusa* have very narrowly separated or contiguous middle coxae, and the intercoxal processes are short with a relatively long, narrow isthmus. In addition, the median lobe of males of *Leptusa* is quite different from that found in most other bolitocharines. I also question Seevers' synonymy of all of Casey's generic names within this subtribe with the European *Bolitochara* Mannerheim. Having seen specimens of all of Casey's genera, I agree that they are almost certainly related to *Bolitochara*, but they differ substantially from specimens of that genus and among themselves, and at least some of

Casey's genera are probably valid. It will take considerable study of relationships within the tribe Bolitocharini to solve this problem. However, the differences in interpretation of the subtribe Bolitocharina used here, and Seevers' group "Bolitocharae" (except perhaps for the position of *Leptusa*) does not seriously affect the possible hypotheses about relationships.

Members of both the Bolitocharina and Gyrophaenina have similarities discussed above shared by other members of the tribe Bolitocharini. In addition, they are also similar in the following characteristics (Figure 151): 1) both have middle coxae which are widely divided by processes from the meso- and metasternum (very widely divided in all gyrophaenines, presumably secondarily narrowed in many bolitocharines); 2) mesosternal process which extends to near middle or just posterior to middle of coxae (assumes character 36 is correctly polarized for the plesiotypic condition for gyrophaenines); 3) a relatively short isthmus (absent in gyrophaenines); 4) mouthpart structure (particularly maxillae) similar, in that both the bolitocharine type and the gyrophaenine type can be derived from a common ancestor; and 5) similar patterns of micro- and macrosetae. It is probably also important that members of both these subtribes are associated with fresh mushrooms or fungi. The gyrophaenines are obligatorially mycophilous and mycophagous. Less is known about the habits of bolitocharines, and their precise relationship to fresh fungi has not been carefully studied. It is apparent from mouthpart structure that bolitocharines are not as highly specialized as fungus-feeders as are gyrophaenines, but they are almost certainly at least facultatively mycophagous.

Although it is not a logical necessity that the sister group of gyrophaenines also be associated with fungi, the most recent common ancestor of gyrophaenines and their sister group must have had mycophilous habits. It would, therefore, not be suprising if the sister group of gyrophaenines was also associated with fresh fungi. In mouthpart structure and habits, members of the subtribe Bolitocharina satisfy most of the characteristics which might be predicted for the plesiotypic sister group of the gyrophaenines.

Again, it is impossible to be certain which of the characteristics shared by bolitocharines and gyrophaenines are true synapotypies. However, gyrophaenines do not share a similar suite of characters with any other group of aleocharines.

Mycophily and mycophagy are certainly highly derived conditions among aleocharines. However, the mycophilous habits of members of these two subtribes may be parallel modifications in response to a similar habitat. While this is a possibility, the hypothesis that mycophily in these two subtribes is derived from a common ancestor with mycophilous habits can be falsified only by showing that either the bolitocharines or the gyrophaenines show at least one well established apotypy with some third group of aleocharines not shared by the other subtribe. At the present state of knowledge, no such synapotypy is known.

The bolitocharines have become longer, narrower insects. This is reflected in the less transverse shape of the pronotum. Derived states of Characters 26, 28, 29 and 30 are an integrated system relating to this narrowing. These characteristics are developed in parallel in the "Gyrophaena" lineage of gyrophaenines. In addition, the bolitocharines have modified the setose area on Tergum 10 to a chevron-shaped area (42 C).

Most modifications in gyrophaenines have apparently been in response to increased mycophagy and involve development of the spore brush of the maxilla. These modifications of the maxilla include 1) truncation of the apex of the lacinia (18); 2) increase in number and density of teeth on truncated area of lacinia (19); and 3) decrease in number of teeth and spines on inner face of lacinia as the manipulative function of the inner face decreases (20). Additional modifications within the Gyrophaenina are discussed below.

#### 4.2.2.4 The subtribe Gyrophaenina as a Monophyletic Group

The hypothesis that members of the subtribe Gyrophaenina as considered here constitute a monophyletic group is supported by at least two strong synapotypies: 1) modification of the maxilla as a spore gathering structure; and 2) presence of a lateral plate on the neck of the spermatheca. Modification of the maxilla is an integrated complex of characters. In the most plesiotypic condition known among gyrophaenines, this complex involves modifications of the apex of the lacinia from acute to obliquely truncate (18 *B*), increase in number and density of lacinial teeth (19 *B*), and reduction of number of teeth and spines on the inner face of the lacinia (20 *B*). Further modifications of this structure within the gyrophaenines reflect increased specialization for feeding on the hymenium layer of mushrooms.

A lateral plate on the neck of the spermatheca (44 *B*) characterizes females of all gyrophaenines examined. Although the structure of the spermatheca has not been well investigated, no similar structure is known to occur in any other group of aleocharine. This lateral spermathecal plate is almost certainly a uniquely derived character state within the gyrophaenines and, as such, provides strong evidence that they form a monophyletic group. Structure of the maxilla of gyrophaenines is unlike any other known among aleocharines. Because all known gyrophaenines are obligatory mycophages, it is a reasonable possibility that this maxillary structure represents parallel modifications for fungus feeding in two or more aleocharine lineages. However, two things support the hypothesis that the similarity is a synapotypy. As noted above, the modification for spore feeding actually involves a complex of characters. That such a large group of characters would be indistinguishably modified in parallel in two or more distantly related lineages seems unlikely. Secondly, as far as presently known, congruence between maxillary modifications and presence of the lateral spermathecal plate in females is universal among gyrophaenines. Therefore, mouthpart structure is best interpreted as a uniquely derived character within the gyrophaenines.

The hypothesis that contiguous mesosternal and metasternal processes (37 *B*) is an apotypy for the subtribe Gyrophaenina is dependent on the assumption that a slight isthmus in members of *Agaricochara* is secondarily derived. This seems reasonable because of the uniformity of the derived condition among all other gyrophaenines.

#### 4.2.2.5 Relationships of *Probrachida* and *Brachida*, and the "Brachida" Lineage as Sister Group to the Remainder of the Gyrophaenines

While specimens of *Probrachida* and *Brachida* have apotypic states of many character, they are quite primitive, particularily their mouthparts. Specimens of *Probrachida* have the most plesiotypic mouthparts among gyrophaenines.

These two lineages likely diverged early in phylogeny of gyrophaenines, but their exact relationships are problematical, because it is difficult to place *Brachida*. Because of the plesiotypic character states retained by *Probrachida*, it is apparent that this group must occupy a basal position in any reconstructed phylogeny of known extant gyrophaenines. In contrast, the position of *Brachida* can be reasonably interpreted in two ways. Alternatives are depicted in Figures 252 and 253.

Hypothesis I– In the first hypothesis (Figure 252), *Probrachida* is considered to be the sister group to all other gyrophaenines including *Brachida*, and within this group *Brachida* is sister to the remainder. The principal assumptions are that loss of teeth from the inner face of the lacinia (20 $B_2$) and reduction of medial setae of the labium from two to one (25 $B_1$) has occurred only once among gyrophaenines.

Under this hypothesis, the lineage which led to *Probrachida* is characterized by ten apotypic character states as opposed to hypothetical states of these characters in the ancestor of the "Brachida and all other gyrophaenines" lineage. These apotypic states include: body setae numerous, dense, uniformly distribued, and long and silky (1 $B_1$); lack of medial microsetae on head (16 *B*, *C*) (assumes loss of apically bifid mandibles in some species); undivided, broadly rounded ligula (24 *C*); pronotum without bisinuate hind margins (26 *B*); pronotal shape more or less broadly oval or subquadrate (28 $B_1$, $B_2$); apico-lateral margin of elytron not sinuate (32 $B_2$); prosternum without a medial ornamentation or transverse carina (34 $C_2$); mesosternal process reaching posterior border of coxa (36 *B*); and spermatheca with an elongate neck proximal to the lateral plate (45 *C*). In addition, *Probrachida* retains four plesiotypic character states in relation to all other gyrophaenines. These include: antennomere 4 similar to 5-10 (8 *A*) (assumes independent derivation of apotypic states of this character in some *Probrachida*); retention of a few scattered teeth on inner face of lacinia (20 $B_1$); retention of numerous rows of setae on apex of galea (22 *A*); and two medial setae on the labium (25 *A*).

Members of the lineage "Brachida and all other gyrophaenines" share apotypic states of: antennomere 4 similar to 1-3 (8 *B*); absence of teeth from the inner face of lacinia (20 $B_2$); rows of setae on galea fewer than in *Probrachida* but greater than 4 and closely spaced (22 $B_1$); and one medial seta on labium (25 $B_1$).

Within the lineage "Brachida and all other gyrophaenines", *Brachida* is characterized by nine apotypic states: long, dense, silky pubescence (1 *B*); apex of right mandible bifid (16 *B*); ligula undivided and broadly rounded (24 *C*); hind margin of pronotum not bisinuate (26 $B_2$); pronotal shape more or less broadly oval or subquadrate (28 $B_1$, $B_2$); apico-lateral margin of elytron not sinuate (32 $B_2$); prosternum without medial ornamentation or transverse carina (34 $C_2$); mesosternal process reaching to posterior border of middle coxae (36 *B*); and spermatheca with neck elongate proximal to the lateral plate (45 *C*). Members of *Brachida* retain eight plesiotypic states relative to all other gyrophaenines. These include: presence of a large number of setae on labrum (in addition to the basic four rows) (9 *A*); labral seta A.L.1 and A.L.2 distant from lateral edge of labrum (14 *A*); presence of an internal setose area on each side of midline of labrum (15 *A*); setae on inner face of lacinia numerous and scattered, or few and scattered (21 *A*, $B_1$); setae on apex of galea numerous, in more than 4 rows (22 $B_1$); setae on apex of galea setiform (23 *A*); setae on metepisternum numerous, irregularly scattered (39 *A*) (assumes independent evolution of apotypic states of this character in some *Brachida* species); and setae on Tergum 10 setiform, unmodified (43 *A*).

Hypothesis I is weakened by the requirements of parallel development of apotypic states in nine characters in *Probrachida* and *Brachida*: numerous, dense, long, silky microsetae (1 *B*); setose area internally on each side of midline of labrum (15 *B*); one or both mandibles apically bifid (16 *B*, *C*); undivided, broadly rounded ligula (24 *C*); pronotum more or less broadly oval or transverse (28 $B_1$, $B_2$); apico-lateral margin of elytron not sinuate (32 $B_2$); prosternum without medial ornamentation or transverse carina (34 $C_2$); and mesosternal process extended to posterior border of middle coxa (36 *B*). In addition, this hypothesis implies that the pair of medial macrosetae on the head are independently lost from *Probrachida* (4 *B*); some species of *Brachida* have antennomere 4 similar to 5-10 (8 *A*); and some *Brachida* have independently evolved spatulate setae on the galea (23 *B*).

Hypothesis II- Hypothesis II (Figure 253) considers *Probrachida* and *Brachida* sister groups, with the two together forming the sister group to the remaining extant gyrophaenines. The principal assumption of this hypothesis is that the broad, undivided ligula is a synapotypy between *Probrachida* and *Brachida*. Under this hypothesis these genera share eight apotypic character states: right mandible apically bifid (16 *B*); (implies that both mandibles bifid (16 *C*) and mandibles not bifid (16 *A*) are additional derived states within *Probrachida*); undivided, broadly rounded ligula (24 *C*); pronotum more or less broadly oval (28 $B_1$); and mesosternal process reaching posterior border of middle coxa (36 *B*).

Members of this lineage retain nine plesiotypic character states not found among other gyrophaenines, including: antennal article 4 similar to 5-10 (8 *A*); large number of setae in addition to major rows on labrum (9 *A*); setae A.L.1 and A.L.2 distant form lateral edge of labrum (14 *A*); teeth on inner face of lacinia few and scattered, but present (20 $B_1$); setae on inner face of lacinia numerous and scattered (21 *A*); setae on apex of galea in numerous , close rows (22 *A*); setae on apex of galea long, setiform (23 *A*); medial setae of labium two (25 *A*); setae on metepisternum numerous, irregularly scattered (39 *A*); and setae on Tergum 10 setiform, unmodified (43 *A*).

If *Probrachida* and *Brachida* form a monophyletic group, then parallel evolution of apotypic states of a number of characters between members of this lineage and other gyrophaenines is required. If antennomere 4 similar to 5-10 (9 *A*) is plesiotypic for this lineage, then modification of antennomere 4 to be similar to 1-3 (9 *B*) must have occurred independently in some species of both *Probrachida* and *Brachida*, and in the ancestor of all other gyrophaenines. Teeth on the inner face of the lacinia (20 $B_1$) in members of *Probrachida* suggests that members of the ancestor of *Probrachida* and *Brachida* must have had this condition. If so, loss of these teeth (20 *B*) must have occurred independently in *Brachida* and the ancestor of all other gyrophaenines. If numerous scattered setae on the inner face of the lacinia (21 *A*) is plesiotypic for the lineage, then reduction in number (21 *B*) must have occurred independently in some species of *Probrachida*, *Brachida* and the ancestor of the remaining gyrophaenines. Similarily reduction of number of setae on the inner face of the lacinia to a single row must have occurred independently in some species of *Brachida* and a number of other gyrophaenine lineages; reduction in number of rows of setae on the galea (22 $B_1$, $B_2$) in *Probrachida*, *Brachida* and the ancestor of the other gyrophaenines; and modification of these setae to plate-like structures (23 *B*) in a few species of *Brachida* and the ancestor of the other gyrophaenines. In addition, two medial setae on the labium (25 *A*) of all members of *Probrachida* suggest that the ancestor of *Probrachida* and *Brachida* must have had this condition. If this is so, then reduction to one such seta occurred in both *Brachida* and the ancestor of all other gyrophaenines. Finally, reduction in number of setae on the metepisternum to two irregular rows (39 $B_1$) or a single well defined row (39 $B_2$) must have occurred in species of *Brachida* as well as in several other lineages.

Hypothesis II is weakened in particular by the requirement of independent evolution of character states 20 $B_2$, 21 $B_2$, and 25 $B$, in at least some species of *Brachida* and the ancestor of the remaining gyrophaenines. However, based solely on number of required parallel evolutionary modifications, this is a more parsimonious hypothesis than Hypothesis I. Also, the lineages of both *Probrachida* and *Brachida* can be derived from an ancestor having a number of relatively plesiotypic character states in relation to the ancestor of the other gyrophaenines. Presence of some species in both *Probrachida* and *Brachida* which have plesiotypic character states and others which have apotypic states suggests that parallelism, probably in response to similar habit, is common.

These considerations lead me to accept Hypothesis II, given the present state of knowledge.

The *Probrachida-Brachida* lineage is arbitrarily and informally designated the "Brachida" lineage.

Members of the "Brachida" lineage retain a number of plesiotypic conditions found in no other gyrophaenines. In particular, the retention of teeth and numerous, scattered setae on the inner face of the lacinia, and numerous rows of unmodified, filiform setae on the apex of the galea of *Probrachida*, are the most plesiotypic conditions of maxillary structures found in known gyrophaenines.

Within the "Brachida" lineage, both *Probrachida* and *Brachida* are hypothesized to be monophyletic lineages based on autapotypic states of several characters. Autapotypic conditions in *Probrachida* include: posterior margin of pronotum medially notched (27 *B*), and neck of spermatheca elongated proximal to the lateral plate (45 *C*). Autaptypic states in *Brachida* include: presence of a single medial seta on the labium (25 $B_1$); absence of teeth from inner face of lacinia (20 $B_2$); and neck of spermatheca elongated distal to the lateral plate (45 *B*). In addition, specimens of each genus have distinctive ground plans for the median lobe of the aedaegus. These two basic aedaegal types may have been derived from that found in a common ancestor. However, the type found in males of *Brachida* is extremely aberrant in relation to that found among other gyrophaenines (see discussion under this genus), and it seems unlikely that it would have been derived from an ancestral type very similar to that found in males of *Probrachida*. It seems most reasonable to hypothesize that in many characters, males of *Probrachida* and *Brachida* are each derived in relation to a common ancestor.

### 4.2.2.6 The Remainder of the Gyrophaenina ("Sternotropa" and "Gyrophaena" lineages) as a Monophyletic Group

The group made up of the "Sternotropa" and "Gyrophaena" lineages contains most of the species in the subtribe. Within the ancestor of these lineages, most of the highly derived characteristics typical of adaptation of gyrophaenines for an intimate association with fresh mushrooms must have developed.

Ten strong autapotypies support the hypothesis that the members of the "Sternotropa" and "Gyrophaena" lineages together form a monophyletic group (Figures 253, 254). Apotypies in the ancestor of these two lineages are: modification of antennal article 4 to be similar to 1-3 (8 *B*); reduction of the number of setae on the labium to the basic rows (9 *B*); labral setae A.L.1 and A.L.2 proximal to the lateral margins (14 *B*); absence of teeth on inner face of lacinia (20 $B_2$); setae on inner face of lacinia few and scattered (21 $B_1$); setae on apex of galea in 4 well separated rows (22 $B_2$); setae on galea spatulate or plate-like (23 *B*); a single median seta on labium (25 $B_1$); setae on metepisternum reduced to two irregular rows (29 $B_1$); and setae on Tergum 10 setiform but short and stubby (43 $B_1$).

Distribution of character states within the "Sternotropa" and "Gyrophaena" lineages suggests that the common ancestor must have retained states of a number of characters which are plesiotypic for the gyrophaenines as a whole. These include: numerous, more or less short, uniformly and densely distributed microsetae (1 *A*); apex of both mandibles simple (16 *A*); hind margin of pronotum markedly bisinuate (26 *A*); pronotum markedly transverse (28 *A*); lateral borders of pronotum more or less deflexed (29 *A*) so that hypomera are not visible in lateral aspect (30 A); apico-lateral borders of elytra markedly sinuate (32 *A*); prosternum markedly transverse (33 *A*), with a median ornamentation (34 *A*); mesosternum with a carina (35 *A*); meso- and metasternal processes meeting near the middle of the mid coxae (36 *A*) with a smooth well developed suture (38 *A*); and spermatheca simple, without an elongate neck (45 *A*).

Concordance of apotypic states in mouthpart characters (particularly 20 $B_2$, 21 $B_1$, 23 *B*, and 25 $B_1$) in all species of these two lineages is strong evidence for monophyletic origin of the "Sternotropa" and "Gyrophaena" lineages. As discussed earlier, because all members of these lineages are, as far as is known, obligatorily mycophagous on fresh mushroom fruiting bodies, there is the possibility of parallel development in mouthpart structure. However, to date the known apotypic states of these character are congruent among all members. That indistinguishably similar apotypies could be derived independently in many characters seems a less parsimonious hypothesis than that all were developed in the same ancestor. To falsify the hypothesis that these two lineages form a monophyletic group would require that variation be found in the shared apotypies listed above (particularly in mouthparts) which would indicate that they were developed in parallel. In addition, if new strong apotypies are found which are incongruous with apotypic states of the mouthpart characters, it would suggest that similarity in mouthpart structure may have evolved in response to similar habits rather than derived from a common ancestor.

### 4.2.2.7 The "Sternotropa" lineage

The "Sternotropa" lineage (Figure 255) is comprised of the genera *Sternotropa* Cam., *Pseudoligota* Cam., *Adelarthra* Cam., *Agaricomorpha* n.gen., *Brachycara* Shp., and *Neobrachida* Cam. In addition, the most parsimonious cladistic placement of *Agaricochara* Kraatz is in this lineage. These 7 genera (with the possible exception of *Agaricochara*) appear to have a monophyletic origin.

The principal assumptions in the hypothesis of a monophyletic origin for this group is that the deeply bifid ligula has been derived only once in the gyrophaenines. It is important that the bifid ligula (24 $D_1$, $D_2$, *E*) is the only apotypy shared by all members of the "Sternotropa" lineage. Similarity of this structure in members of *Sternotropa*, *Pseudoligota*, *Agaricomorpha* and *Brachycara* provides evidence that the bifid ligula is of monophyletic origin at least in these groups. However, variation in detailed structure of the bifid ligula, particularly in the rather robust lobes of the ligula in specimens of *Adelarthra*, the elongate apically bifid ligula of specimens of *Neobrachida* and the slightly divided ligula of *Agaricochara* species, suggests that bifurcation may have occurred more than once among the gyrophaenines. Also, all members of the "Sternotropa" lineage for which natural history information is available are inhabitants of woody polypores. Therefore the hypothesis that a bifid ligula may in some way be associated with living or feeding on polypores is a distinct possibility.

The possibility that the bifid ligula has been derived more than once is especially serious because of lack of strong apotypic states of other characters in members of this lineage. Additional apotypic states might show congruence or discordance with distribution of the bifid ligula and would provide a test for hypotheses about the monophyletic origin of this character state.

Members of the "Sternotropa" lineage are all very similar in general body form. However, this similarity is best interpreted as the result of symplesiotypy, as discussed below.

Modification of the setal patch on Tergum 10 to an inverted-V or chevron-shaped patch (or distinct rows) (43 $C_1$, $C_2$) in most of the species in this lineage may be taken as an additional apotypy for this lineage. However, presence of a square setal patch (42 *B*) in some species suggests that the ancestor of the "Sternotropa" lineage had a square patch. This tendency to form a chevron-shaped patch may be an "underlying synapotypy" (Saether 1979). It is impossible to distinguish between true underlying synapotypies (reflecting genetic similarity) and parallelisms resulting from strong selection pressure for similar features. The chevron-shaped patch on Tergum 10 has been derived so commonly among members of this lineage that it is tempting to suggest some underlying genetic similarity among these insects. However, it is also important to remember that they all appear to live in a similar habitat, polypore mushrooms.

*Neobrachida* and *Adelarthra* show variation in structure of the bifid ligula, but share apotypic conditions of several characters (discussed more fully below) with some other members of the "Sternotropa" lineage. This provides additional evidence that they are members of this lineage, and that the bifid ligula is actually a shared synapotypy among members of this lineage.

*Agaricochara* is tentatively placed in this lineage by the slightly divided ligula. However, members of this genus share a number of similarities with the "Gyrophaena" lineage. Therefore, alternative hypotheses about the position of *Agaricochara* within the cladogram may be postulated. These alternatives are discussed more completely below, but since the bifid ligula is the only apotypy shared by *Agaricochara* with other members of the "Sternotropa" lineage, it provides no additional information about the origin of this character state.

In spite of problems with this character, because of present lack of evidence to the contrary, I accept the hypothesis that the bifid ligula is uniquely derived in the ancestor of the "Sternotropa" lineage. However, the monophyly of this lineage is not strongly established, and a search for additional character states which will support or negate this hypothesis is needed.

The "Sternotropa" lineage is particularly characterized by retention of plesiotypic states of nine characters in most species of the lineage. These plesiotypies include: base of pronotum markedly bisinuate (26 *A*); a markedly transverse pronotum (28 *A*); lateral borders of pronotum more or less deflexed (29 *A*) so that the hypomera are not visible in lateral view (30 *A*); apico-lateral borders of elytra markedly sinuate (32 *A*); prosternum with a medial knob, carina or tubercle (34 *A*); mesosternum carinate (35 A); and setae on metepisternum in two irregular rows (39 *B*) not delineated anteriorly or ventrally by a carina (40 *A*).

Common retention plesiotypies, in addition to a large percentage of the members of the "Sternotropa" lineage being small to very small, dark, weakly limuloid beetles, densely covered with short microsetae, give the members of this group a rather uniform appearance. Such similarity in a large number of character states among members of a group, all of which appear to occupy a similar habitat, suggests the possibility that these character states are similarities derived in response to a common environmental stimulus, and thus are apotypies rather than plesiotypies. However, neither in-group nor out-group comparisons support this hypothesis (see character analysis above). Until additional evidence encourages re-evaluation of character analysis and polarities within the gyrophaenines, it seems most reasonable to hypothesize that general similarity in habitus among members of the "Sternotropa" lineage is mostly due to widespread retention of plesiotypies.

#### 4.2.2.7.1 Relationships of *Agaricochara*

The cladistic relationship of *Agaricochara* within the gyrophaenines is uncertain. As indicated above, two hypotheses can be reasonably proposed at the present time. The monophyletic lineage which led to *Agaricochara* may have originated soon after origin of the "Sternotropa" lineage; if so, it is the sister group to all remaining members of this lineage (Figure 255). Alternatively, it may have originated near the base of the "Gyrophaena" lineage (Figure 259). Neither of these hypotheses is markedly supported. If the hypothesis that *Agaricochara* is a member of the "Sternotropa" lineage is accepted, then it is a highly autapotypic member. In particular, in the apotypic states of this genus, it shows a great deal of parallelism with members of the "Gyrophaena" lineage. Apotypic character state present among members of *Agaricochara* shared in parallel with the base of the "Gyrophaena" lineage include:

prosternum without a tooth, carina or knob (34 *B*); and setae on metipisternum in a single well defined row (39 $B_2$). Characters shared in parallel with some members of the "Gyrophaena" lineage but not found in any other member of the "Sternotropa" lineage include: a more or less broadly oval pronotum (28 $B_1$); lateral borders of pronotum not markedly deflexed so that hypomera are narrowly visible in lateral aspect (30 $B_1$) (shared with a few members of the "Sternotropa" lineage); prosternum with a faint transverse carina (34 $C_1$); and setose area on metepisternum delimited anteriorly and ventrally by a faint carina (40 *B*).

Placement of *Agaricochara* within the "Sternotropa" lineage is very tentatively accepted in this study. Most of the apotypic character states that members of *Agaricochara* share with members of the "Gyrophaena" lineage are either reductions or likely to be subject to parallelism (see discussion under "Gyrophaena" lineage). However, evidence for this conclusion is weak and contradictory, and considerable additional study of relationships of members of this genus is required to more confidently place it among the gyrophaenines.

The remainder of the "Sternotropa" lineage is hypothesized to form a monophyletic group on the basis of common possession of a deeply divided ligula (24 $D_2$). The elongate apically divided ligula of *Neobrachida* is probably an autapotypic condition within this lineage. This portion of the "Sternotropa" lineage is naturally divided into two monophyletic lineages: 1) a lineage including *Sternotropa*, *Pseudoligota*, *Adelarthra* and tentatively *Neobrachida*; and 2) a lineage including *Agaricomorpha* and *Brachycara*.

### 4.2.2.7.2 Relationship of *Sternotropa*, *Pseudoligota* and *Adelarthra*

This grouping of genera (Figure 255) is hypothesized to be monophyletic based on the common possession by males of a highly autapotypic condition of the median lobe of the aedeagus (46). This aedeagus type is characterized by origin of a long filiform flagellum near the basal bulb. In most species the flagellum forms a loop proximally around the basal bulb and is extended distally in a groove in the functionally ventral surface of the aedeagus. This aedeagus type is very distinctive and is found in no other group within the Gyrophaenina. It appears to be strong evidence that this is a monophyletic group.

In comparison to the sister lineage of the group, the ancestor of *Sternotropa*, *Pseudoligota* and *Adelarthra* must have retained several plesiotypic states including: setal patch on Tergum 10 square with few setae (42 *B*); and setae on Tergum 10 short and stubby, but setiform, not flattened (43 $B_1$).

Within this lineage, *Sternotropa* and *Pseudoligota* are hypothesized to be sister lineages based on common possession of the characteristic type of aedeagal median lobe described above, and also by autapotypic conditions of the parameres (Character 47). In males of both genera, two of the setae of the apical sclerite of the parameres are located far towards the base of the sclerite, and are disproportionately large (Figures 227, 229).

Within the lineage *Sternotropa-Pseudoligota*, *Sternotropa* is hypothesized to be monophyletic based on common possession by members of this genus of a distinct chevron-shaped setal patch on Tergum 10 (42 $C_1$) (modified to form distinct, well developed rows of setae in some species (42 $C_2$), and the subspatulate shape of the setae of Tergum 10 (43 $B_2$). Monophyly of *Pseudoligota* is supported by the absence in all members of this genus of a mesosternal carina (35 *D*); a fused meso-metasternal suture (38 *B*); and slighly impressed abdominal terga (41 $B_1$, $B_2$).

### 4.2.2.7.3 Relationships of *Adelarthra*

*Adelarthra* is a highly autapotypic member of this monophyletic group of genera, and its relationship to *Sternotropa* and *Pseudoligota* is uncertain. To properly evaluate character state distribution among these genera, three hypotheses are considered (Figures 256A-C). Hypotheses I and II are dependent on whether a fused suture between the meso- and metasternal processes (38 *B*) is a synapotypy among members of *Pseudoligota* and *Adelarthra*, or whether it has evolved in parallel in these two genera.

Hypothesis I (Figure 256A) is based on the assumption that fused meso-metasternal processes have been evolved in parallel in the ancestors of these genera. In this situation, there is no synapotypy uniquely shared by members of any pair of genera. Postulation of an unresolved trichotomy is unavoidable. In hypothesis II (Figure 256B) it is assumed that the presence of a fused meso-metasternal process is a synapotypy between members of *Pseudoligota* and *Adelarthra*, with these two genera as the sister group to *Sternotropa*. The sister group relationship between *Pseudoligota* and *Adelarthra* is, however, very inadequately supported by this character state (38 *B*) because of the possibility of indistinguishable parallel development of the apotypic state. In this regard, it is important to note that members of a number of species of *Sternotropa* have independently evolved the fused condition, suggesting that parallelism in this character is common.

If, however, structure and position of the setae on the apical sclerite of the parameres of males of *Pseudoligota* and *Sternotropa*, as described above, is considered uniquely characteristic in members of these genera, then Hypothesis I is transformed into Hypothesis III. Hypothesis III (Figure 256C) states that *Adelarthra* is the sister group to *Pseudoligota* plus *Sternotropa*. This hypothesis is no more parsimonious than Hypothesis II based on number of shared apotypic characters, but Hypothesis III is more likely to be correct because the apotypic condition of the parameres shared by males of *Sternotropa* and *Pseudoligota* is less likely to have been derived in parallel than is the fused state of the intercoxal processes shared by *Pseudoligota* and *Adelarthra*. Therefore, I tentatively accept Hypothesis III as presently the most likely of the possible cladistic relationships between *Adelarthra*, *Sternotropa* and *Pseudoligota*.

*Adelarthra* is highly autapotypic in six characters when compared to members of its sister lineage. These autapotypies include: loss of most body microsetae (1 $C_2$); macrosetae on pronotum, elytra and abdomen extremely large (2 $B_2$); sculpture absent, body intregument smooth (3 $B_2$); lateral margins of pronotum very markedly deflexed (28 $C_2$); and setae on metepisternum very few, restricted to posterior third (39 $C$).

#### 4.2.2.7.4 Relationships of *Neobrachida*

The cladistic relationships of *Neobrachida* are the most inadequately understood of any known group within the "Sternotropa" lineage. This is, in large part, a result of the fact that no specimens of this genus are available for detailed examination, and no males are known. Therefore, structure of the mouthparts is virtually unknown, and nothing is known of the aedeagus or spermatheca. The hypothesis presented in Figure 257 is based on the assumption that the chevron-shaped setal patch on Tergum 10 (42 $C_1$) and flattened, subspatulate setae on this sclerite (43 $B_2$) are shared derived characters between *Neobrachida* and *Sternotropa*. However, this relationship is very weakly founded. Since neither aedeagus nor spermatheca are known, it is not known whether members of *Neobrachida* share the unique aedeagus type (Character 46) of *Sternotropa* and related genera. Therefore, *Neobrachida* may not be related to this group of genera. In addition, structure of the ligula in *Neobrachida* is quite aberrant in relation to other members of the "Sternotropa" lineage.

Alternative placements of this genus include: 1) *Neobrachida* as sister group to *Sternotropa* plus *Pseudoligota*, implying independent derivation of the chevron-shaped setal patch (42 $C_1$) and subspatulate setae (43 $B_2$) in *Sternotropa* and *Neobrachida*; and 2) *Neobrachida* as the sister group to *Sternotropa* plus *Pseudoligota* plus *Adelarthra*, implying the same parallel developments. Neither of these placements can presently be supported by shared apotypic character states.

Little more can be done with the cladistic relationships of *Neobrachida* at present.

### 4.2.2.7.5 Relationships of *Agaricomorpha* and *Brachycara*

This pair of genera is hypothesized to form a monophyletic group (Figure 255). on the basis of two shared character states: setal patch on Tergum 10 chevron-shaped (42 $C_1$); and setae on Tergum 10 subspatulate (43 $B_2$). The uniform distribution of apotypic states of thse two characters among members of *Agaricomorpha* and *Brachycara* contrasts with plesiotypic states of these same characters in many species of the *Sternotropa-Pseudoligota-Adelarthra* group of genera. This indicates that the ancestor of *Sternotropa* and related lineages must have had the plesiotypic state of these characters, while the ancestor of *Agaricomorpha* and *Brachycara* must have had the apotypic state. This supports the hypothesis that these two groups of genera are sister groups.

Only a single autapotypy supports the hypothesis that *Agaricomorpha* is monophyletic and has a sister-group relationship with *Brachycara*. In males of all members of *Agaricomorpha* examined, the apical lobe of the median lobe of the aedeagus is displaced laterally (Figure 215), not otherwise known among the gyrophaenines. It is, therefore, hypothesized to be uniquely derived within this lineage. In other characters, *Agaricomorpha* is markedly plesiotypic in relation to *Brachycara*. If additional study should indicate that the aedeagus type described above is plesiotypic rather than apotypic, or, if it has been derived within some lineage of *Agaricomorpha* rather than in its common ancestor, then *Agaricomorpha* would have to be considered paraphyletic in relation to *Brachida*.

In constast, members of *Brachycara* are markedly autapotypic and the monophyly of this lineage is well supported by seven apotypic features: microsetae short, more or less reduced, body subglabrous (1 $C_1$); integumental sculpture absent, body uniformly smooth (3 $B_2$); lateral borders of pronotum very markedly deflexed (29 $C_2$);

mesosternal carina reduced (35 *B*) or modified to a low ridge (35 *C*); abdominal terga weakly impressed (41 $B_1$); and setal patch on Tergum 10 in distinct chevron-shaped rows (42 $C_2$). The possible hypothesis that members of this genus may be only a highly autoapotypic lineage of *Agaricomorpha* cannot be conclusively rejected because of lack of clear knowledge of polarity in aedeagal characters. However, the median lobe of males of *Brachycara* does not have the laterally displaced apical lobe characteristic of males of *Agaricomorpha*. This suggests that the ancestor of both groups had a more generalized aedeagus than that found in *Agaricomorpha*, and supports the hypothesis that these are sister groups.

#### 4.2.2.8 The "Gyrophaena" lineage

The "Gyrophaena" lineage is comprised of three genera: *Phanerota* Csy., *Eumicrota* Csy., and *Gyrophaena* Mann. (Figure 258). Structural evidence supports the hypothesis that these three genera have a monophyletic origin. In addition, some evidence suggests that *Agaricochara* may be a member of this group. However, as discussed above, *Agaricochara* may also be interpreted to be a member of the "Sternotropa" lineage.

No single strong apotypy supports the hypothesis that the "Gyrophaena" lineage forms a monophyletic group. Instead, there are a number of moderately useful to relatively weak derived character states shared in concordance by members of this lineage. Most important among these hypothesized apotypies is the undivided, protruded ligula (24 *B*) characteristic of all members of the lineage. If this is actually a derived condition of the ligula among gyrophaenines, then it offers strong support that these genera have a monophyletic origin. However, as discussed in the character analysis (Section 4.1.2), this character state may also be interpreted as most similar to the character state from which the ligula type of other gyrophaenines was derived. If so, then common possession of this character state would provide no evidence about cladistic relationships. As indicated in the character analysis, at present the simple protruded ligula is not easily interpreted as an apotypic condition within the gyrophaenines. Nevertheless, even if this character state is interpreted as plesiotypic within gyrophaenines, it does not seriously affect the hypothesis that the "Gyrophaena" lineage is monophyletic.

Other apotypic character states shared by members of the "Gyrophaena" lineage in contrast to the "Sternotropa" lineage include: setae on the inner face of lacinia in a single well differentiated row (21 $B_2$); prosternum without a medial ornamentation (34 $B_2$); mesosternum without a medial carina (35 *D*); setae on metepisternum in a single well differentiated row (39 $B_2$); and setae on Tergum 10 flattened and more or less subspatulate.

In comparison to the "Sternotropa" lineage, members of the "Gyrophaena" lineage form a very diverse assemblage. The distribution of hypothesized plesiotypic conditions among members of this lineage suggest that the ancestor of the "Gyrophaena" lineage must have retained the following plesiotypic conditions.: microsetae numerous, more or less short, densely and uniformly arranged (1 *A*); uniformly reticulate sculpture (3 *A*); hind margin of pronotum markedly sinuate (26 *A*); pronotum transverse (28 *A*); lateral borders of pronotum more or less deflexed (29 *A*) so that hypomera not or only narrowly visible in lateral aspect (30 $B_1$, $B_2$); elytron markedly sinuate (32 *A*); markedly transverse prosternum (33 *A*); meso- and metasternal processes of similar length, meeting near the middle of the midcoxae (36 *A*); and the setal patch of Tergum 10 more or less square with numerous setae (42 *A*). In addition, given the remarkable diversity of basic aedeagal forms within the "Gyrophaena" lineage, the ancestor must have had a relatively plesiotypic aedeagus. At present, great diversity of aedeagal form precludes reconstruction of important features of the ancestral type.

### 4.2.2.8.1 Relationship of *Agaricochara* within the "Gyrophaena" lineage

If the slightly divided bifid ligula of specimens of *Agaricochara* is hypothesized to have been derived independently from the similar state in members of the "Sternotropa" lineage, then *Agaricochara* shares several apotypic conditions with members of the "Gyrophaena" lineage. These apotypies include: prosternum without medial ornamentation (34 *B*); mesosternum without a carina (35 *B*); and metepisternum with setae in a single, well differentiated row (39 $B_1$). Multiple origin of these character states in a number of well established lineages indicates that parallelism in these characters is common. At present, it seems most reasonable to assume that the bifid ligula is a uniquely derived character state within the gyrophaenines. Character states shared by members of *Agaricochara* and the "Gyrophaena" lineage would then be parallelisms (Figure 259).

### 4.2.2.8.2 Relationships among *Eumicrota*, *Phanerota* and *Gyrophaena*

Among these genera, *Eumicrota* is hypothesized to be the sister group to *Phanerota* plus *Gyrophaena* (Figure 258). The hypothesis that the members of *Eumicrota* form a monophyletic group is supported by presence in all members of the genus of two unique apotypies. The setal patch on Tergum 10 is modified to a distinct V-shaped patch (42 *D*). This state is unknown in other gyrophaenines. Also, to my knowledge, it has not been reported among other aleocharines. In complete concordance with this character state is the fact that males of *Eumicrota* have a very distinctive aedeagal form, characterized by: a long, slender, often coiled flagellum; an elongate, slender apical process, often with a terminal knob or angulation; and a small basal bulb with a small, oval depressor plate placed far back on the proximo-ventral surface (Figure 197). This basic form is not obscured by interspecific variation.

This group of small to very small, dark beetles retains a number of character states which are plesiotypic for the "Gyrophaena" lineage. These include: numerous, more or less short and densely arranged microsetae (1 *A*); very small macrosetae (2 *A*); hind margin of pronotum markedly bisinuate (26 *A*); pronotum markedly transverse (28 *A*); and apico-lateral angles of elytra markedly sinuate (32 *A*).

The monophyly of the *Phanerota-Gyrophaena* lineage is weakly supported by several character states: macrosetae large, easily distinguished from microsetae (2 $B_1$); hind margin of pronotum at most weakly bisinuate (26 $B_1$); and apico-lateral margins of elytra weakly bisinuate (32 $B_1$). Within this pair of genera, *Phanerota* is highly autapotypic. Autapotypic character states found in members of *Phanerota* include: body setae small, reduced in number, body subglabrous to more or less glabrous (1 $C_1$, $C_2$); eyes extremely large (7 *B*); pronotal hind margin not at all sinuate (26 *B*$_2$); spermatheca with neck elongated proximal to lateral plate (45 *C*); and a distinctive aedeagal form (Figure 195, 196), showing little variation among species (Character 46). There seems little doubt that *Phanerota* is a monophyletic assemblage.

There are no known uniquely derived character states shared by all members of the genus *Gyrophaena* to indicate that it is monophyletic relative to *Phanerota*. Therefore, at present, *Gyrophaena* must be considered paraphyletic in relation to *Phanerota*. This lack of unique apotypies may be a result of the extreme heterogeneity among the species now included in the genus. Diversity of body form within *Gyrophaena* is as great as the total range found among all other members of the Gyrophaenina. Within *Gyrophaena* are found species whose members are markedly plesiotypic in most characters, to those which are markedly apotypic. Still, many monophyletic lineages can be recognized within *Gyrophaena*. Some of these may deserve generic status. However, revision of the generic status of *Gyrophaena* will require a phylogenetic study of the world fauna. This is a task of monumental difficulty in a group as diverse and inadequately known as *Gyrophaena*.

I retain *Phanerota* as a distinct genus for two reasons, even though it makes *Gyrophaena* as presently defined paraphyletic. First, I believe that additional study of *Gyrophaena* will result in it being divided into several monophyletic genera, one of which will probably be the sister group to *Phanerota*. Secondly, retaining *Gyrophaena* as a paraphyletic group graphically illustrates the need for study of this group at the world level.

### 4.2.2.9 Uncertain placement: *Encephalus*

The cladistic relationships of *Encephalus* cannot be determined at this time. Members of *Encephalus* are highly autapotypic. They share with members of the "Brachida" lineage a markedly robust body form, long mesosternal process (*B*), broadly rounded ligula (*C*), and, apparently, siimilar habits (see Section 3.1.2.2). However, they share with members of the "Gyrophaena" lineage a single medial seta on the labium ($B_1$), structure of the maxilla (particularly, a single distinct row of setae on inner face of lacinia and four distinct rows of flattened setae on apex of galea), and glabrous body integuments ($C_2$). In addition, the aedeagus, especially the median lobe, is very similar to that of members of the *Gyrophaena nana* species group of Seevers (1951), as are the secondary sexual characeristics of males. Which of these similarities are parallelisms cannot be presently ascertained.

As discussed in Section 3.3.3.4, the New Zealand species of *Encephalus* may not be closely related to the Holarctic species, and perhaps should be placed in a separate genus. The elongate, entire ligula, prosternum with a distinct transverse carina, and maxillary structure, suggest these may be members of the "Gyrophaena" lineage.

# 5. Evolutionary Trends

## 5.1 Introduction and Methods

A wide variety of staphylinids visit fresh mushrooms, and are commonly collected there in great abundance and diversity. However, most mushroom visitors appear to be predaceous on other arthropods which occur there. Most, indeed, are attracted to a mushroom after it begins to decay. Some of these staphylinids may be truly mycophagous, and others may feed on the fungus facultatively. However, except for members of the few groups mentioned below, this has not been conclusively shown.

Among those staphylinids commonly found on mushrooms, gyrophaenines are unusual in that both larvae and adults are exclusively mycophagous. Since most staphylinids are predaceous, obligate mycophagy is a relatively rare, and apparently highly derived, habit within this family. Because of lack of knowledge of habits of most staphylinids, it is not known how many times obligate mycophagy has been independently derived. However, at present, I know of only two lineages of staphylinids conclusively known to be obligate fungus feeders in both larval and adult stages. The first of these are members of the subfamily Oxyporinae. All of these are included in a single genus, *Oxyporus* Fab., of world-wide distribution. Members of this genus are large, colorful beetles as adults, and both larvae and adults burrow into and feed on the flesh and gill tissue of fleshy mushrooms (Campbell 1969, and personal observations).

The other known lineage of mycophagous staphylinids is the Gyrophaenina. The members of this subtribe are additionally unusual among fungivorous insects in that they are adapted to feed exclusively on the spore producing layer (the hymenium) of fresh mushrooms. This is a very important aspect of the relationship of gyrophaenines to mushrooms. There are a great many insects which feed on the flesh of fresh mushrooms, but most of these feed by burrowing into the flesh of the gills, stem or cap. Populations of insects feeding within the flesh are often very high, and both intra- and interspecific competition must often be quite intense in this habitat. Adaptation to feed exclusively on the hymenium allows gyrophaenines to use a spatial and nutritional resource within the mushroom habitat not extensively used by other mushroom inhabiting insects. Thus, gyrophaenines avoid many of the direct interspecific competitive interactions common within the mushroom habitat. Indirect competition with other mushroom inhabitants still occurs, since any of the activities of these other organisms which influences productivity of the hymenium in turn affects gyrophaenines (see Section 3.1.2.3 for a more detailed discussion of this).

This characteristic feeding habit of gyrophaenines combined with the unique characteristics of mushrooms as habitats have apparently provided opportunities for extensive radiation within the lineage, resulting in a group of great world-wide diversity. However, the radiation of gyrophaenines has produced some oddly disjunct evolutionary patterns, particularly in distribution of gyrophaenines among various mushroom groups.

In this chapter, I examine, in a very general way, evolution of the more important structural features which allow gyrophaenines to use the mushroom habitat in this unusual way. Then, by considering some of the more obvious general patterns of distribution of gyrophaenines within mushroom groups, I form generalizations and hypotheses about how these relationships between gyrophaenines and fresh mushrooms may have evolved.

To keep perspective, it is important to remember that life history and habits, host relationships, and systematics of gyrophaenines are incompletely known. Any generalizations made in this section are considered provisional and may require modification with additional study. The intent here is to develop initial hypotheses which provide a framework for formulation of specific questions about the evolution of gyrophaenines.

The basic method for inferring evolutionary pathways of diversification has been discussed by Anderson (1979). Fundamental to this approach is the method of phylogenetic systematics (Hennig 1965, 1966; Ross 1974 and others), which allows hypotheses to be formed about phylogenetic relationships without requiring assumptions about specific evolutionary processes. Each monophyletic lineage is therefore a "natural" group in that it has a unique history. Such a system of relationships provides a base for making hypotheses about evolutionary diversification in structural, functional, ecological and other characteristics.

Anderson (1979) outlined the steps in deciphering "pathways of evolutionary divergence". These need not be repeated in detail here. The basis is that monophyletic terminal taxa are arranged in increasingly more comprehensive monophyletic groups on the basis of shared uniquely derived characters (synapomorphies). Results are depicted on a cladogram. Then additional data (ecological, structural, behavioral, etc.) are overlaid on the cladistic relationships and hypotheses developed about the evolutionary processes involved in diversification of the group. This method is used here to develop hypotheses about evolution of mouthpart structure and diversification of gyrophaenines in major host groups of mushrooms.

Detailed discussion of the phylogenetic analysis of the genera of gyrophaenines is presented in Section 4.2.2. The most parsimonious hypothesis of these cladistic relationships presently available is summarized in Figure 260. Two genera, *Encephalus* Kraatz and *Neobrachida* Cameron, are of uncertain placement and are not included in the cladogram.

Major features of this cladogram of importance in subsequent analysis include:

1. the hypothesis that members of the subtribe Bolitocharina (= Group Bolitocharae of Seevers, 1978) form the sister group to the Gyrophaenina;
2. members of the Gyrophaenina form a monophyletic lineage;
3. within Gyrophaenina, three major lineages can be recognized, arbitrarily and informally designated the "Brachida" lineage, the "Sternotropa" lineage and the "Gyrophaena" lineage.

## 5.2 Mushrooms as Habitats

### 5.2.1 Introduction

Since gyrophaenines are obligatory inhabitants of fresh mushrooms, an understanding of general features of the mushroom habitat and the insects which occupy such a habitat is essential to unravelling major features of the evolution of gyrophaenines.

Much of the information about insects associated with fungi and most generalizations about characteristics of the mushroom habitat are derived from investigations on fungicolous Coleoptera (e.g., Benick 1952; Donisthorpe 1935, 1939; Lawrence 1973; Minch 1952; Paviour-Smith 1959, 1960, 1965,1969; Rhefous 1955; Scheerpeltz and Höfler 1948; Weiss 1920a, 1920b, 1920c; Weiss and West 1920, 1921). Additional information is available from studies of fungicolous Diptera (Buxton 1960), and from faunistic studies of individual lignicolous fungi. For example, insects associated with *Pitoporus betulinus* (Bull. ex Fr.) Karst. have been studied by Paviour-Smith (1960), Pielou (1966), and Pielou and Verna (1968); *Fomes formentarius* (Linn. ex Fr.) Kickx. by Matthewman and Pielou (1971) and Pielou and Matthewman (1966); and various woody bracket fungi by Graves (1960). Other natural history studies of individual mushroom-inhabiting insects such as those of *Bolitotherus cornutus* (Heatwohle and Heatwohle 1968; Liles 1956; Pace 1967) and *Tetratoma fungorum* F. (Paviour-Smith 1964,1965) provide additional information.

Elton and Miller (1954) grouped the fungus habitat into their "General System" with other small decomposing habitats, which included dying and decaying wood, carrion, dung, animal and small human artifacts, and slime molds. Elton (1966) noted that fungi form concentrated habitats which are ephemeral and interspersed within major habitats. He divided the resources available in fungi into spores, living fungus tissue, hard bracket fungi, and soft decaying fungi. He also pointed out that for analysis, whether the insects found on fungi were fungus feeders, wood borers, bark feeders, parasites, or accidental visitors, must be distinguished.

Scheerpeltz and Höfler (1948) recognized that, as habitats, fungi could be conveniently divided into hard forms on wood, soft forms on wood, and soft forms on the ground. They further divided soft fungi on the ground into five stages according to the state of development or decomposition. They suggested that as fungi pass through these successional stages, they alter as habitats for insects.

Paviour-Smith (1959, 1965) extended and modified Scheerpeltz and Höfler's stages to include stages in growth and decomposition of lignicolous fungi. Additionally, she discussed the importance of the consistency of a fruiting body both when alive and upon decomposition and desiccation after death, as factors which may affect suitability as a breeding site for insects.

Hingley (1971), in studies of *Daldina concentrica* (Bolt. ex Fr.) Ces. & Not., found that succession begins with a more host specific fauna and continues with more generalized fungus feeders and predators as the habitat characters of the mushroom change with age. In later stages, insects typically associated with fungi were replaced by those more typical of decaying wood.

Major fruitings of fungi may occur throughout the spring, summer or autumn, with particularly large fruitings after heavy rains in late summer and early autumn. After the fruiting body is fully developed, fertile spores from the hymenium are released. Following spore release, most soft fungi decay as a result of the action of bacteria and microfungi. Many polypores persist and produce additional releases of spores, often in response to wet weather.

The mode and rate of decomposition of mushrooms is dependent both on hardness ("woodiness") and location. Most ground fungi are in a humid microclimate and therefore deliquesce rapidly on decay. Rate of decomposition is dependent on a number of factors, including specific mushroom involved, temperature and humidity, and rainfall. Decay may be accelerated by burrowing and feeding activities of fungivorous Diptera and other arthropods. Also, exposure and trauma to inner tissues of the mushroom due to mechanical injury by slugs, birds or small mammals may speed decomposition. Most lignicolous fungi contain binding hyphae, and sometimes skeletal hyphae, and are therefore of tougher consistency than ground fungi. Most sporophores are also raised off the ground and are continually exposed to air currents. As a result, most fruiting bodies desiccate with age, and, upon death, become shrivelled or friable in texture. However, if such lignicolous fungi fall to the ground or become sodden, they decompose at a rate and in a mode similar to that of ground fungi.

Rate and mode of decomposition of different mushrooms are of importance to gyrophaenines, since they can inhabit only fresh mushrooms.

### 5.2.2 General Characteristics of Mushrooms as Habitats

The mushroom habitat is actually a range of microhabitats dispersed within a more inclusive habitat, which have a number of similar characteristics to which any group of animals using them must respond. In general, mushrooms are:

1. ephemeral (many highly so)
2. unpredictable in time and space
3. extremely heterogeneous in physical and chemical characteristics.

It is difficult to think of another set of habitats having this particular combination of characteristics. In particular, extreme chemical and physical heterogeneity found among mushrooms makes them unusual as temporary habitats.

Overlaid on these general characteristics are specific differences resulting from different rates and modes of decay, hardness, physical and chemical characteristics, seasonality, microdistribution, and abundance of members of individual mushroom species.

### 5.2.3 Requirements for Use of the Mushroom Habitat

As discussed in relation to the life cycle of gyrophaenines in Section 3.1.2.2.2.8, many of the structural and natural history features of gyrophaenines are a response to unique features of the mushroom as a habitat. Exploitation of habitats with the general characteristics of mushrooms requires that gyrophaenines have unusual specializations. First, gyrophaenines must be able to determine when mushrooms are or are likely to be present in the general vicinity. This could present a problem, since gyrophaenines appear to become relatively inactive when mushrooms are rare (see Section 3.1.2). Inability to predict location and time of occurrence of individual mushrooms is important in this respect. While it may be possible for members of a gyrophaenine species to be adapted to become active when mushrooms are most likely to be present (e.g., after rains at certain times of the year) or restrict their activities to areas in which they are most likely to encounter mushrooms (certain microhabitats within a forest), it seems unlikely that they are able to adapt to predict location and time of occurrence of individual fruiting bodies or mushrooms of a particular species. For perspective, it is important to remember that for an animal the size of a gyrophaenine, distance between suitable mushrooms may be relatively very long even when mushrooms are common.

Associated with the general unpredictable characteristics of individual species or fruiting bodies is the requirement that gyrophaenines detect that mushrooms are available for colonization and distinguish suitable from unsuitable mushrooms quickly. It is important to emphasize that as far as is known, gyrophaenines must feed, mate, lay eggs, and larvae must mature on an individual fruiting body before it decays.

The extreme chemical and physical heterogeneity of mushrooms is a very important contraint on gyrophaenines. Because of the general unpredictability of mushrooms, it would be ideal if members of a gyrophaenine species could use any mushroom encountered. However, it seems unlikely that members of any single gyrophaenine species could have the necessary range of physiological and structural adaptations which would allow efficient use of every mushroom encountered. Therefore, it seems more likely that only a very limited subset of available mushrooms are suitable for habitation by members on any particular gyrophaenine species. This substantially increases the difficulty for individual gyrophaenines in finding a suitable host.

Additionally, since numbers of individual mushroom species and diversity and species composition of the mushroom flora may vary seasonally, yearly or geographically, gyrophaenines must have some adaptive means of maintaining themselves whenever suitable fungi are not available.

Finally, of major importance is the physical and physiological ability to harvest the nutritional resources of the mushroom habitat while at the same time avoiding or overcoming competition with other organisms which are involved in similar activities.

## 5.3 Adaptations to the Mushroom Habitat

### 5.3.1 Morphological Adaptations

#### 5.3.1.1 Adaptations for Resource Use

While association of gyrophaenines and fresh mushrooms is highly developed, gyrophaenines are not substantially different in body form and habitus from aleocharines with less specialized habits (but see Section 5.3.1.2 below). The principal structural adaptations of gyrophaenines to mushrooms involve modifications of the mouthparts. In particular, the maxilla appears to be the main feeding structure, and is highly modified for eating the hymenium layer of fresh mushrooms. This may be the key structural adaptation of gyrophaenines, since it allows them to use the mushroom habitat in a very unusual way and subsequently affects other characteristics of the beetle-mushroom association.

Characteristics of the adult maxilla are illustrated in Figures 73, 235 and others. (Here I describe only the adult structure. Structure of the maxillae of larval gyrophaenines parallels that of adults in both structural and functional characteristics to a remarkable degree. This is discussed in more detail below.) The general features of the gyrophaenine maxilla illustrated by Figure 73 include the following:

1. Apex of the lacinia is truncate, with a well

differentiated patch of small, densely arranged teeth or spines, which I refer to as the "spore brush".

2. Inner face of the lacinia lacks teeth or spines.
3. Setae on the inner face of the lacinia are in a single, well defined row.
4. Setae on the apex of the galea are in four well separated rows.

In addition, the galeal setae are modified to subspatulate or plate-like structures (Figure 235).

Gyrophaenines feed by "grazing" maturing spores, basidia, cystidea and hyphae from the hymenium layer. This is apparently primarily accomplished by scraping the hymenium surface with the spore brush. The galeal setae form a cap over the apex of the lacinial spore brush and may prevent loss of material removed from the hymenium.

The function of the mandibles in feeding is unclear. Gyrophaenine mandibles are not highly modified to eat fungus in relation to those of less specialized aleocharines. However, they may function to remove food from the spore brush, form it into a bolus, and/or grind food.

It is possible to arrange known maxillary forms of gyrophaenines and closely related bolitocharines into a transformation series, as shown in Figure 261. Transformation in a number of different character systems can be seen. These include:

1. Modification of the apex of the lacinia from more or less acute to obliquely truncate. Associated with this

is modification of the teeth on the apex of the lacinia from a loosely organized patch, weakly differentiated from spines and setae on the internal face of the lacinia to a distinct, well organized patch of small, closely spaced teeth (*A*→*B*);

2. Progressive loss of teeth from the inner face of the lacinia (*A*→*B*→*C*).
3. Reduction in setae on inner face of lacinia to a single row (*A*→*B*→*C*→*D*).
4. Reduction in number of rows of setae on galea from numerous, closely spaced rows to four well separated rows (*A*→*B*→*C*).
5. Modification of galeal setae from filiform to subspatulate or plate-like (*A*→*B*→*C*).

These modifications probably reflect increasing reliance on hymenium scraping as a feeding mechanism. Associated with this seems to be progressive loss of manipulative and grasping functions of the face of the lacinia as reflected by loss of teeth and spines in this area.

By superimposing these maxillary modifications on a simplified phylogeny of gyrophaenines, it is possible to make a tentative hypothesis about how hymenium feeding may have arisen in the gyrophaenine lineages.

Figure 262 shows the distribution of maxillary forms among the major lineages of gyrophaenines. Members of the subtribe Bolitocharina have maxillae with many relatively generalized features for aleocharines as a whole. Maxillae of members of the subtribe are probably more similar to those present in the common ancestor of bolitocharines and gyrophaenines than any maxillary form found among the gyrophaenines. Though bolitocharines inhabit fresh mushrooms, structure of the maxilla seems to indicate that they are not as highly specialized for fungus feeding as are gyrophaenines. As noted above, the exact relationship of bolitocharines and fresh mushrooms is unknown.

By time of origin of the gyrophaenines, the lacinial spore brush was well differentiated but some scattered teeth remained on the inner face of the lacinia; setae were numerous and scattered on the inner face of the lacinia; and galeal setae were unmodified and in numerous rows. Maxillae with these features characterize some members of the "Brachida" lineage. In general, maxillae of members of this lineage are the most plesiotypic found among gyrophaenines. It is important to note that feeding habits of members of this lineage are unknown. The habitat of the large majority of species in this lineage has not been recorded. While some members are occasionally found on mushrooms on logs (Benick 1952), they are more commonly collected from moldy leaf litter or rotting grass tufts (Lohse 1974, and others). Possibly, members of this lineage do not have an obligatory association with fresh mushrooms. The less highly derived mouthparts of members of the "Brachida" lineage are consistent with this hypothesis. This presents the possibility that adaptations in the maxilla of gyrophaenines may have been developed in response to general fungus feeding and later were modified to feed specifically on the hymenium layer of fresh fruiting bodies.

By time of origin of the ancestor of the "Sternotropa" plus "Gyrophaena" lineage, all the highly derived character states of the maxilla of gyrophaenines had developed (except for retention of scattered setae on the inner lacinal face in some members of the "Sternotropa" lineage). Uniformity of derived states in mouthpart structure among members of these two lineages, particularly complete loss of teeth from the inner face of the lacinia, a well differentiated, dense spore brush on the apex of the lacinia, and reduction of galeal setae to four well separated rows of flattened setae, suggests that by time of origin of the ancestor of these lineages, gyrophaenines were fully committed to feeding on the hymenium of fresh mushrooms. This hypothesis is supported by the fact that all members of the "Sternotropa" and "Gyrophaena" lineages for which data are available are found in large numbers only in association with fungi, particularly fresh fruiting bodies.

It appears, therefore, that evolution of the characteristic way that gyrophaenines use the mushroom habitat is reflected in modifications in the maxilla. The early gyrophaenines may not have had an obligatory association with fresh mushrooms. Evolution of the ability to feed exclusively on the hymenium of mushrooms was apparently a later adaptation. This hypothesis is, of course, very sensitive to whether or not the major features of the proposed cladogram are correct. Falsification of aspects of the cladogram would require modification of these hypotheses.

Too little is yet known of structural variation in larval gyrophaenine mouthparts to allow a similar analysis of the evolution of these structures. However, the structural similarities between adult and larval maxillae strongly suggest that larvae of gyrophaenines are adapted to the use the mushroom habitat in a way very similar to that of adults. Structural parallels in maxillae of larval and adult gyrophaenines are remarkable (compare Figures 237 and 243). The spore brush on the apex of the mala of larval gyrophaenines is similar in all important respects to that found on the lacinia of adults. Additionally, it seems reasonable to hypothesize that the leaf-like scale at the outer apical angle of the mala of larvae may perform a function similar to that of the rows of subspatulate setae on the galea of adult gyrophaenines.

Interestingly, habitat-related structural variations in adult maxillae discussed below are reflected in larval mandibles. This further suggests that larval mandibles are under a similar selective regime.

### 5.3.1.2 Habitat Related Structural Features

In this section I discuss structural characteristics of gyrophaenines which seem to be correlated with differing features of the various types of mushrooms occupied by them. Though these features appear to be correlated with various types of mushrooms, their origin is uncertain. Therefore, as discussed below, there are other possible explanations for these features than adaptation in response to selection.

Gyrophaenines associated with either persistent polypore or ephemeral gilled mushrooms tend to have a suite of external features which cause beetles most commonly found on mushrooms of either of these groups to have a similar habitus. It is important to emphasize that the correlation under discussion here is a tendency for gyrophaenines occurring in similar habitats to display similar external features. Exceptions are known, but the pattern of similarity is striking in spite of these. Members of those groups most commonly found on woody polypores tend to be, or have:

1. small size (the smallest gyrophaenines are in this group).
2. dark color, usually unicolorous piceous, black, brown or red-brown.
3. more or less sublimuloid body form or abdomen sides converging from base to apex.
4. body densely, uniformly covered with small microsetae.
5. macrosetae short, inconspicuous (but not in some

*Sternotropa* and *Adelarthra*).

6. pronotum markedly transverse.
7. pronotum with hind borders markedly to moderately bisinuate.
8. pronotum lateral borders deflexed so that hypomera invisible in lateral aspect.
9. apico-lateral angles of elytra markedly to moderately sinuate.

In contrast, members of those groups of gyrophaenines most commonly found on fleshy gilled mushrooms tend to be, or have:

1. larger size.
2. generally lighter color, often bicolorous, with both lighter and darker areas on same beetle.
3. more or less parallel-sided body.
4. microsetae on body fewer; head, prothorax and abdomen subglabrous.
5. macrosetae more prominent, larger.
6. pronotum less transverse.
7. pronotum with base slightly to not bisinuate.
8. pronotum lateral edges less deflexed so that hypomera moderately to broadly visible in lateral aspect.
9. apico-lateral angles of elytra slighty to not sinuate.

Information about details and variation on these generalizations can be found by referring to the comparative morphology section (3.1.1) or the generic descriptions (Section 3.3.3).

Whether cause and effect are involved in these correlations is not clear. Uniform structural features among members of a group may result from selection for similar characteristics by features of the habitat, similar phylogenetic ancestry, or both. Marked correlation of these external features with polypore or gilled mushroom habitats suggests that contrasting characteristics of the habitats may be selecting for these features. However, it has been argued in Section 4.1.2 that for each of the features correlated with polypore mushroom habitats, except size and color, the out-group comparisons within aleocharines suggest that they are best interpreted as ancestral (plesiotypic) within Gyrophaenina. Small size and dark color may be adaptations to features of the polypore habitat, but this is difficult to evaluate without additional data.

If these suppositions are correct, then those structural features correlated with gilled mushroom habitats are in some way selected for by the habitat. This hypothesis is further correlated by the relative phylogenetic position of the gyrophaenine groups which occur most commonly on gilled mushrooms (see Section 5.4.2 and Table 4). Additionally, within the heterogeneous assemblage of species presently included within *Gyrophaena*, different species are known which have external features typical of gyrophaenines from either polypore and gilled mushrooms. These seem to correlate well with the patterns of host preference described above. For example, members of

*Gyrophaena hubbardi* Seevers and related species which are apparently most common on polypores, are difficult to separate on superficial external characters from members of the "Sternotropa" lineage.

Possibly, adaptations for life between gills of mushrooms in constant contact with the hymenium layer are involved in producing a tendency to have similar features in those gyrophaenines which live on gilled mushrooms. At present the data are much too tenuous and scattered to allow this set of correlated features to be evaluated further. Additional study is needed to determine if these patterns remain intact under detailed scrutiny and to determine detailed features of the various types of mushroom habitat.

A second interesting correlation of structure with polypore and gilled mushroom habitats involves details of the maxillary structure of adult gyrophaenines. Those gyrophaenines which live on woody polypores have a lacinial spore brush with relatively more numerous closely spaced, shorter teeth (Figures 236) in comparison to those living on gilled mushrooms (Figures 234). The most closely spaced, numerous teeth in the spore brush known to me characterize adults of *Brachycara* species (Figures 94, 237). Members of *Brachycara*, as far as is known, live only on polypores.

It seems reasonable to hypothesize that these differences in number and density of the teeth in spore brushes of gyrophaenines are in some way related to the different problems for feeding presented by polypore and gilled mushrooms. Hardness of the mushroom, and size, shape or accessibility of spores and the hymenium layer are possible factors contributing to this structural difference.

An additonal interesting correlation is the tendency for those gyrophaenines which occupy polypores to have V-shaped or chevron-shaped setal patches on tergum 10. while those which are most common on gilled mushrooms have more or less square setal patches (see sections on comparative morphology and phylogenetic analysis for details). It is particularly interesting that a chevron-shaped setal patch appears to have been evolved at least twice in the "Sternotropa" lineage. It is not possible to evaluate this correlation further at this time. However, it is possible that the setal patch on tergum 10 is involved in cleaning behavior. If so, it suggests that the problems of keeping the integument clean may be different in the two types of mushrooms.

All of the correlations between habitat type and structure of gyrophaenines require additional study outside the range of this investigation. They are reviewed here primarily to introduce the interested student to other areas of gyrophaenine evolution and natural history which could be profitably investigated.

### 5.3.2 Life Cycle and Behavioral Adaptations

Life cycle and behavioral adaptations of gyrophaenines to the mushroom habitat are discussed in more detail in Section 3.2.2. However, it is important to emphasize here that many of the features of the life cycles and behavior of gyrophaenines are almost certainly a direct result of the nature of mushroom habitats. Rapid colonization of fruiting bodies is apparently an adaptation in response to the ephemeral nature of mushrooms. The possibility of active aggregation of gyrophaenines discussed in Section 3.1.2.1.2 may be an adaptation to a combination of unpredictability and ephemerality of mushrooms. If a suitable mushroom were discovered by a member of a gyrophaenine species, attracting other gyrophaenines of the same species to the mushroom might both increase the mating success of the original individual on the mushroom and more efficient and quicker use of available mushrooms. However, at present, because too little is known of aggregation in gyrophaenines and effects of intraspecific competition among gyrophaenines, it is difficult to evaluate scenarios which would allow aggregation to evolve.

Mating on mushrooms may also be related to their ephemeral nature, but it may also be an adaptation resulting from increased efficiency of mating when many gyrophaenine adults are present on a single fruiting body. The limited circumstantial evidence that the preoviposition period is short and oviposition occurs soon after colonization is consistent with what might be expected from requirements of an ephemeral habitat. A prediction might be that females mated on one mushroom would colonize another and oviposit without mating again, but this has not been investigated.

Very rapid larval development is almost certainly an adaptation to the ephemeral nature of mushrooms. Associated with this is rapid initiation of feeding and apparently more or less continuous feeding activities described for larvae of *Phanerota fasciata* (Ashe 1981a).

It seems reasonable to expect that those gyrophaenines which live on more persistent polypore mushrooms may be under less stringent requirements for very rapid colonization of fruiting bodies and rapid life cycle. This would, therefore, suggest that life cycle and behavior of those gyrophaenines which live on polypores may differ in minor or significant ways from those which live on gilled mushrooms.

Presence of adult gyrophaenines in moist litter and under logs may be an adaptation to survive when few or only unsuitable mushrooms are available for colonization.

As discussed below (Section 5.4.4), the general patterns of host relationships of gyrophaenines are also likely to be adaptations to characteristics of the mushroom habitat.

## 5.4 Patterns of Host-Mushroom Relationships

### 5.4.1 Introduction

As Seevers (1951) pointed out, the problem of host relationships is important. In particular, an understanding of gyrophaenine evolution appears impossible without consideration of the origin of both broad and detailed features of host relationship patterns. I have, therefore, within the limitations of this study, attempted to gather host information for gyrophaenines and apply it to problems relating to gyrophaenine evolution.

Very little has been published about host relationships of gyrophaenines, especially for the North American fauna. Host lists for European gyrophaenines include Benick (1952) [all known records for Palearctic Region], Donisthorpe (1935) [England] and Scheerpeltz and Höfler (1948) [Austria].

For North America, the literature about hosts of gyrophaenines is notable by its absence. Insect inhabitants of various woody bracket fungi have been relatively well studied by Matthewman and Pielou (1966), Graves (1960), Graves and Graves (1966), Pavior-Smith (1960), Minch (1952) and Pielou (1966). However, none of these mentions finding any beetles of the subtribe Gyrophaenina. Relatively few papers have been written describing insects of gilled mushrooms. These include Moennick (1939, 1944), Chagnon (1935) and Weiss and West (1920, 1921). Of these, Weiss and

West (1920) list one host for *Gyrophaena* (=*Eumicrota*) *corruscula* (Erichson), and Moennick (1939, 1944) lists hosts for *Gyrophaena* (=*Phanerota*?) *fasciata* Say and *Gyrophaena flavicornis* Melsh. Ashe (1981a) has listed hosts for *Phanerota fasciata* (Say), and (in press) hosts for *P. dissimilis* (Erichson).

Few of those who have examined the hosts of gyrophaenines have attempted to discern a pattern in those host relationships. An exception is Scheerpeltz and Höfler (1948). Also, White (1977) has attempted a general treatment of which mushrooms are most likely to form acceptable hosts for gyrophaenines. However, much of the understanding of the way fungus beetle host relationship patterns develop is from studies of beetles of the family Ciidae which occur on woody polypores (Paviour-Smith 1960; Lawrence 1973).

Except where otherwise noted, the host-mushroom data presented in this section were collected by me incidental to collecting for systematic research. A single collection is here considered to be all the specimens collected from a single mushroom or from a closely associated group of mushrooms of the same species on the same day. Biases inherent in data collected and handled in this way include:

1. Relative abundance of different mushroom species makes uniform sampling of all available mushrooms difficult.
2. Number of fruiting bodies sampled per collection affects average number of beetles per mushroom.

3. Groups or clusters of mushrooms tend to attract more attention than single mushrooms.
4. Pooling of data from a number of fruiting bodies of the same mushroom species, even if closely associated, can obscure potential differences in the *Gyrophaena* fauna due to different ages of fruiting bodies, competition or possibly other factors.
5. Host information gathered while collecting for systematic research gives only limited data about the mushrooms on which gyrophaenines do not occur.

However, in spite of such potential biases, these data include more than 700 individual collections with host data and reflect predictable trends of abundance and distribution of gyrophaenines among mushrooms. These data provide patterns for a first analysis of gyrophaenine host relationships. However, more sophisticated analysis of host relationships will require data collected in a more rigorous way.

Mushrooms were identified using a number of popular and semi-popular identification guides. These included Smith (1958), Hesler (1960), Kauffman (1971), Smith and Smith (1973), Smith, Smith and Weber (1979), and others. Confident identification of many mushrooms to species is difficult for the non-specialist. I have, therefore, consistently been conservative in my identifications of fungi. If specific determination is in question, I have been satisfied with a generic determination in which I have confidence. Whenever possible I have collected voucher specimens of host fungi so that many host records can be verified or identified more precisely.

Patterns of host relationships can be discussed at a number of taxonomic levels. Each one of these levels provides different insight into evolution of gyrophaenines. In this section, I consider host relationships at three taxonomic levels: 1) intergeneric patterns, 2) broad intrageneric trends with the large genus *Gyrophaena*, and 3) interspecific patterns.

### 5.4.2 General Distribution of Gyrophaenines among Mushroom Groups

The distribution of gyrophaenines within available mushrooms is surprising. There are many groups of fungi which produce macroscopic fruiting bodies (commonly called "mushrooms") on which gyrophaenines are virtually never found. These include stinkhorns (Phallales), bird's-nest fungi (Nidulariales), puffballs and earthstars (Lycoperdales), coral mushrooms (Clavariaceae), jelly fungi (Heterobasidiomycetes) and cup fungi (Ascomycetes). Other mushroom groups on which gyrophaenines are rare and which are probably rarely or never included among the preferred hosts of gyrophaenines, include the bolete mushrooms (Boletaceae) and the tooth fungi (Hydnaceae).

Reasons for absence of gyrophaenines from some fungi (stinkhorns, puffballs, jelly fungi) appears to be related to the fact that the spore producing tissue is not generally available. Absence from others (coral fungi, ascomycetes) has no obvious reason.

When considered in the perspective of all possible mushroom groups, gyrophaenines are found on a very limited selection of mushrooms. They are common only on members of the Polyporaceae of the Aphyllophorales, the pored mushrooms, and several families of the Agaricales, the gilled mushrooms. These two general groups of mushrooms differ mainly in that the hymenium of members of the Polyporaceae is produced on the inside of pores, while that of the Agaricales is produced on the surface of lamellae or gills.

For gyrophaenines, polypores and gilled mushrooms differ in a number of potentially important general characteristics. Habitat differences of probable importance to gyrophaenines are summarized in Table 3, and discussed more fully with possible consequences in Sections 3.2.2.2 and 5.3. It is important to note here that mushrooms of these two groups differ in persistence, place of spore production, and rate and length of time of spore production. These two extremes of habitat characteristics are joined by a range of more or less persistent gilled mushrooms and more or less ephemeral polypores. However, these contrasts suggest that, at least potentially, responses to the different conditions of thse two major mushroom types could produce marked differences in life cycle, habits and population structure, and, subsequently, evolution of those gyrophaenines which occupy them.

With these characteristics and possible consequences of the characteristics in mind, it is possible to examine patterns of distribution of gyrophaenines among mushrooms.

### 5.4.3 Intergeneric Host Patterns

At the very broadest level of host relationships that has any information, it is possible to consider occurrence of genera among major habitat types of mushrooms, which are subjective categories suggested by the criteria of habitat characteristics discussed above.

Table 4 is a generalized summary of the distribution of members of gyrophaenine genera among major habitat types within the mushrooms. Mushroom data have been collected by me except that the information for *Agaricochara* is from Scheerpeltz and Höfler (1948), Benick (1952) and Donisthorpe (1935), and that for *Pseudoligota* from label data and published habitat data (Cameron 1920, 1939). This table predicts that members of *Sternotropa* occupy woody polypores, although no data are available. The number of crosses refers to the relative number of species in that genus which are most common or limited to mushrooms of a particular type.

Table 4 indicates that it is possible to recognize four broad host groups among mushrooms inhabited by gyrophaenines. Group I is made up of those gyrophaenines for which nothing is known of the host relationships. Primarily this includes the members of the "Brachida" lineage. As discussed above, it is possible that members of this lineage do not have an obligatory association with fresh mushrooms. Group II is made up of those gyrophaenines which are restricted to woody polypores. This includes all members of the "Sternotropa" lineage for which information is available, some members of *Eumicrota*, and a few *Gyrophaena*. Group III includes those which are most common on fleshy polypores. Gyrophaenines which occupy mushrooms of this type usually have host ranges which overlap into the persistent gilled mushrooms and woody polypores. Gyrophaenines which occupy Group III type habitats include most *Eumicrota* and some *Gyrophaena*. Group IV is made up of those gyrophaenines which are restricted to or most common on gilled mushrooms. This includes the most members of *Gyrophaena* and *Phanerota*.

It is obvious that most genera of gyrophaenines occupy polypores. However, it is possible that this is a taxonomic artifact (see Section 3.3.3). In contrast, the gilled mushrooms have been invaded only by the lineage which leads to *Gyrophaena* and *Phanerota*. However, it is among the gyrophaenines which occupy gilled mushrooms that the great species diversity occurs, mostly in the genus *Gyrophaena*.

This distribution of gyrophaenines among broad mushroom groups along with evolution of structural adaptations in feeding structures discussed above suggests that as a first hypothesis about broad trends, it is possible to consider gyrophaenine evolution as attainment of a series of adaptive zones. Phylogenetic relationships suggest that the ancestor of the "Sternotropa" and "Gyrophaena" lineages probably lived on polypore mushrooms. This hypothesis is strengthened by the fact that gyrophaenines which prefer to occupy polypores are found in both lineages. In contrast, the phylogenetic position and great species diversity of those groups which live on gilled mushrooms suggests that it is possible to consider evolution of the ability to use the more ephemeral and unpredictable habitat of gilled mushrooms as the attainment of a new adaptive zone, which was followed by extensive radiation. However, hypotheses about whether attainment of the adaptive zone is clade or grade based (has occurred only once or by a number of lineages) must await more complete systematic studies of the heterogeneous assemblage of species now included in the genus *Gyrophaena*. This problem arises because presence of some species within *Gyrophaena* which occur on polypores suggests that gilled mushrooms may have been invaded several times during the evolution of this lineage.

### 5.4.4 Intrageneric Level Host Patterns

One of the most interesting characteristics of host patterns of gyrophaenines is the major groups of mushrooms within generally acceptable mushroom types which they rarely or never occur on. Table 5 provides a subjective diagram of the general distribution of members of the major species groups of *Gyrophaena* and *Phanerota* which occur on members of commonly encountered gilled mushroom families. This is compiled from my own host records for North American gyrophaenines and may not generalize to other areas with a different gyrophaenine fauna. Lack of records of gyrophaenines from members of a mushroom group does not indicate that gyrophaenines have not been collected on these mushrooms. Instead, it indicates that only isolated adult specimens have been collected and there is no indication that gyrophaenines ever occur on these mushrooms in large numbers. Table 5 shows that gyrophaenines have a curiously disjunct distibution within the available mushrooms. There are major groups of mushrooms, the families Lepiotaceae, Hygoporaceae, Agaricaceae, and Coprinaceae, which produce fruiting bodies, but which are seldom inhabited by gyrophaenines. In addition, not apparent from Table 5, is the fact that often, even within a single genus of mushrooms, the same disjunct patterns of gyrophaenine distribution may be found. Some species attract large numbers of gyrophaenines while others have few or no gyrophaenines on them.

There is no correlation between known physical and chemical characteristics of mushrooms and this distribution. Gyrophaenines occur on a large number of mushroom species which are known to be toxic, for a varienty of reasons, to humans, and fail to occur on others which are innocuous, or even desirable food for humans.

It is also apparent from Table 5 that members of a species group are usually most common on one or a few mushroom families rather than being distributed generally throughout available mushrooms.

While these general patterns of distribution of gyrophaenines within gilled mushrooms are quite baffling at present, it is obvious that gyrophaenines are establishing criteria for characteristics of an acceptable mushroom host in an unexpected way.

### 5.4.5 Species Level Host Patterns

The simplicity of a subjective diagram of distribution of gyrophaenines within mushroom groups such as that presented in Table 5 is belied by the complexity of host data when the distribution of individual species among available mushrooms is considered.

Presentation of the many hundreds of available host records for gyrophaenines is not possible in this study. However, details of the host records are important. Patterns of relationships only become apparent after a very large number of host records have been examined. Instead, in this section, I present some of the more important patterns of host data that are encountered and give a summary of the host records of gyrophaenine species which illustrate this pattern.

Detailed host data are availble from the author.

Pattern 1 – Adults may be found on a wide variety of often distantly related mushrooms.

This is a very common pattern. Almost always, whenever a large amount of host data is available for a species, the variety of mushrooms on which adults have been found represents many genera and usually several families of mushrooms. This is illustrated by the collection records for *Phanerota fasciata* (Say) (Table 6). In 61 individual collections with host data, adults of this species have been collected on members of 11 genera of mushrooms in 4 families. However, it is important to note that specimens of *P. fasciata* have not been found on all possible mushrooms, including all brown and dark-spored mushroom families and all polypores.

Pattern 2 – Although adults of most species of gyrophaenines occupy a variety of mushrooms, they are usually more common on members of one or a few mushroom genera.

Table 7 summarizes the distribution of adult individuals of *Gyrophaena nanoides* Seevers in 11 collections. While adults of this species have been found on members of 9 genera of mushrooms, large numbers of individuals have been found only on *Cortinarius* species. The collection data for *P. fasciata* also illustrate Pattern 2 (Table 6). Specimens of *P. fasciata* are most commonly collected on members of *Russula* Grey and *Lactarius* (D.C.) ex Grey (family Russulaceae).

Pattern 3 – A very few species of gyrophaenines seem to have a well defined host range.

I have 13 collections of *Gyrophaena egena* Casey with host data. Of these, 9 are from members of *Lactarius*, and 4 are from specimens of *Russula* (total number of specimens, 368). I have not encountered this beetle on any other mushroom, even though I have collected extensively in areas where it is common. *Russula* and *Lactarius* together form a distinctive family of gilled mushrooms, the Russulaceae. This suggests that mushrooms in these genera may have chemical or physical properties of importance to these beetles. Pattern 3 is very uncommon among gyrophaenines, and I know of no other gyrophaenine for which adquate host data are available that show it.

Pattern 4 – There are a few species of mushroom which always support an extremely large population of gyrophaenines representing a large number of species. *Amanita verna* (Fr.) Quel. in the Blue Ridge Mountains of North Carolina seems to be such a mushroom. I have collected 751 adult individuals representing 13 species from a single fruiting body, and, in all, I have collected 17 gyrophaenine species from this mushroom species. *Hypholorna* *fascicualare* Quel. in Europe may exhibit a similar pattern of gyrophaenine habitation (see Benick 1952; Scheerpeltz and Höfler 1948; Donisthorpe 1935; and other host lists of European gyrophaenines).

Pattern 5 – While one may consistently and predictably find members of a species of gyrophaenine on specimens of a particular group of mushrooms, and only occasional specimens on other mushrooms, one may sometimes find them in large numbers on a mushroom from which they have not been collected.

Table 8 summarizes collection data with host records from *Gyrophaena monticola* Seevers. Adults of this species have been commonly collected on mushrooms in three genera of the Cotinariaceae and one genus of Crepidotaceae. This suggests that they prefer light-brown spored mushrooms. However, in one instance they have been collected in large numbers on specimens of *Pleurotus* (Fr.) Quel., a light spored mushroom which occurs on logs. Pattern 5 is commonly encountered and causes much of the problem in interpretation of these host data patterns.

Other data sets show additional patterns, but these seem to be the most common and important ones. (See White (1977) for a more general treatment.) It is apparent from these examples that specific patterns of host relationships between gyrophaenines and mushrooms are very complex.

### 5.4.6 Principal Patterns and Origin of Host Relationships

Although the patterns of host data are complex, the fact that it is possible to recognize any pattern at all indicates that gyrophaenines distinguish between mushroom groups at some level. Though many of these patterns cannot be explained at present, a few generalizations can be made about characteristics of relationships between gyrophaenines and mushrooms. First, all species have a host range — no monophagous species are known. Secondly, host preferences (rather than obligatory relationships) are the rule. When "preferred" mushrooms are not available, "less preferred" mushrooms are used. Finally, adults may live and feed on mushrooms on which they cannot breed. This was originally suggested by Scheerpeltz and Höfler (1948). Circumstantial evidence (personal observations) continues to support this hypothesis, but it has not been carefully tested. Paviour-Smith (1960) proposed that members of the beetle family Ciidae which live in woody polypores have a similar relationship to mushrooms. She proposed the term "headquarters" for the most preferred or commonest breeding mushrooms for the species of ciids in an area.

Probably, all of these general characteristics are responses to the nature of the mushrooms as habitats. In addition ,the mushroom flora may vary tremendously in the course of a season. At times mushrooms are incredibly abundant in great taxonomic diversity. At other times in the season, there are few fruiting bodies or species available. Species composition of the mushroom flora also changes throughout the year. To use this habitat efficiently, gyrophaenines must be able to respond to this variability. Ideally, the ability to use all available mushrooms would be of greatest advantage to a gyrophaenine (Ashe 1981a). This, however, does not appear to happen. The members of a gyrophaenine species apparently use only a limited part of the mushroom flora.

The distribution of gyrophaenines among mushrooms can be partially explained by the tentative hypothesis that members of a species have an evolved tolerance to a range of conditions presented by mushrooms. They will, therefore, tend to occur on any mushrooms which present these conditions (White 1977). Closely related mushrooms will tend to have similar physical and chemical characteristics. Consequently, the same gyrophaenine species are likely to occur on them. However, less closely related mushrooms may also have similar characteristics, at least as far a the characteristics of importance to the gyrophaenines are concerned. These less closely related mushrooms may therefore serve as a suitable host for members of a gyrophaenine species which is more commonly found elsewhere.

Additionally, we should consider the working hypothesis that gyrophaenines distinguish between four broad categories of mushrooms: 1) "preferred hosts"; 2) "acceptable" breeding hosts; 3) "acceptable" adult hosts; and 4) unacceptable mushrooms. The boundaries between these broad categories are probably indistinct, and may vary depending on a variety of conditions. The distribution of available mushrooms would then overlap various portions of these acceptance categories for members of a gyrophaenine species. The way that this might occur is illustrated in the schematic diagram in Figure 263. The two diagrams in this figure show differences in the available mushroom flora which overlap different parts of the acceptability spectrum for all potential mushrooms for a species of gyrophaenine. Such differences in available mushrooms may result from seasonal, geographic or yearly variation.

If this generalization is correct, then several subsequent corollaries are suggested. First, examination of a limited amount of host data may present a confusing array of mushrooms. Patterns of the acceptability spectrum would become apparent only after examination of a large volume of host data. Second, this acceptability spectrum suggests that the preferred host need not be present for the members of a gyrophaenine species to survive. It implies that they are able to respond to variability in available mushrooms as discussed above.

In summary, it appears that at least two factors have had fundamental influence in evolution of the relationship between gyrophaenine staphylinid beetles and fresh mushrooms. First, evolution of a mouthpart structure that allowed the beetles to graze on the hymenium layer of the mushroom rather than feed directly on the fungal flesh opened a relatively unused portion of the mushroom habitat. Gyrophaenines thereby avoided much of the intense competition found among insects which feed on flesh of mushrooms.

Secondly, general characteristics of the mushroom as a habitat require that members of each species of gyrophaenine evolutionarily optimize among conflicting requirements. These include: need to use every mushroom encountered; physiological limitations suggested by the great chemical diversity of mushrooms; and physiological and competitive advantages expected from specialization.

Gyrophaenines seem to have resolved these conflicting requirements by evolving a tolerance to a range of physical and chemical characteristics provided by mushrooms. This tolerance range (reflected in the "acceptability spectrum" of a species) allows members of a gyrophaenine species to respond to seasonal, yearly, and geographic variation in the mushroom flora.

## 5.5 Adaptive Zones and Possible Evolutionary Scenarios

### 5.5.1 Evolutionary Scenarios

Eldredge (1979) defines an evolutionary scenario as "a phylogenetic tree with an overlay of adaptational narrative" (p.192). Scenarios are therefore inductive narratives designed to explain how some particular evolutionary pattern took place. However, he points out that most scenarios are not based on well corroborated phylogenetic trees. They are therefore mostly "fairy tales" based on untestable hypotheses about evolutionary processes or community organization, and do not represent "good science".

He suggests that there are at least two ways to improve scenarios: 1) base them more clearly on phylogenetic trees and 2) eliminate the more purely speculative evolutionary processes from them. If this is done the scenarios can be more informative than simple descriptions of where various groups occur. They become simplified models of major features of evolution of the group, and, as such, may stimulate further investigation. Also, when presented in this way, scenarios are both testable and refutable (Eldredge 1979),

Scenarios are, however, far removed from the original data base from which relationships were hypothesized and numerous additional assumptions have been added. Therefore they may be expected to be wrong in detail. Strict adherents of "hypothetico-deductive" methods in science strongly disagree with *ad hoc* modification of scenarios as details are shown to be incorrect. However, modifications of scenarios to make them more consistent with new data would seem important, or alternately, as suggested by some cladists (Schaeffer, *et. al.* 1972) scenarios should not be constructed at all. With respect to the possible heuristic value of scenarios this latter alternative seems the less desirable of the two.

Much of this confusion is lessened if it is realized that a scenario is not a single hypothesis. It is, instead, a series of hypotheses. It is rare that an entire scenario can be falsified at once. For this to be possible, a very basic assumption in the scenario must be shown to be false. More commonly, one or more less comprehensive assumptions within the scenario are falsified along with the subsequent hypotheses or parts of the scenario dependent on these assumptions. Modification of incorrect assumptions and hypotheses is what leads to the accusation that one is "fixing up" the scenario by *ad hoc* hypotheses. However, it appears that hypotheses in a scenario can be tested as long as the assumptions on which they are based are clearly stated.

An evolutionary scenario can be falsified by at least the following tests:

1. Since an evolutionary scenario is based on a cladogram, the scenario can be falsified by re-evaluation of sister group relationships.

2. Evolutionary scenarios (or specific hypotheses within the scenario) can be falsified by evidence that the ecological or habitat conditions postulated did not exist.
3. An evolutionary scenario can be falsified by additional life history information which indicates that the animals do not behave or relate to the environment in the way postulated.
4. An evolutionary scenario can be falsified by additional distributional data (either habitat or geographic) which are not consistant with the assumptions of the scenario.
5. An evolutionary scenario can be falsified by discovery of fossils for which the distribution in time and space is not consistant with that postulated in the scenario.

Additional tests for specific hypotheses within a scenario may be possible.

### 5.5.2 Adaptive Zones and Major Features of the Evolution of Gyrophaenines

As pointed out by Eldredge (1979), it is very important that evolutionary scenarios be based explicitly on phylogenetic trees (*sensu* Eldredge 1979, and Eldredge and Cracraft 1980). Eldredge and Cracraft (1980) have correctly emphasized that only trees depicting hypothesized patterns of ancestry and descent have any meaning beyond the cladogram level of analysis. Additionally, higher taxa do not show patterns of ancestry and descent in the same context that species do. Therefore, for higher taxa, there is no formal distinction between the cladogram and a phylogenetic tree. Therefore, the phylogenetic tree on which this scenario of gyrophaenine evolution is based is the same as with the cladogram of genera depicted in Figure 260.

Cladistic relationships among gyrophaenine genera (Figure 260) coupled with distribution of major lineages of gyrophaenines among mushrooms (Table 4) suggests that the concept of "adaptive zones" can be useful in understanding how the broad host trends of gyrophaenines may have developed.

The concept of "adaptive zones" (Simpson 1953; Bock 1965) implies that the environment can be considered a mosaic of subhabitats, regions or zones within which characteristic adaptive complexes are required for survival of the organisms occupying those zones. Under this concept, evolution is viewed as acquisition of a specific adaptive complex which makes a series of previously unoccupied habitats (new adaptive zone) available to a group of organisms. Evolution of the adaptive complex is usually taken to occur by a series of adaptive steps by species occupying a "transition zone" of habitats with intermediate characteristics. Of particular importance is attainment by a group of organisms of a zone that they were previously unable to occupy, and their subsequent diversification within that zone.

Under these criteria the major habitat types provided by mushrooms can be considered to represent a series of adaptive zones for gyrophaenines. Mushrooms provide a range of habitats from relatively persistent woody polypores to very ephemeral fleshy gilled mushrooms. More or less fleshy ephemeral polypores and more or less persistent gilled mushrooms provide a transition zone between these two habitat types.

Limited data suggest the following scenario. Lack of precise knowledge of the habits of members of the subtribe Bolitocharina and members of the "Brachida" lineage makes speculation about early history of gyrophaenines very uncertain. However, it seems reasonable to expect that gyrophaenines descended from an ancestor which was in some way associated with fungi, either obligatorily or facultatively. This ancestor may have fed facultatively on fungus mycelium and spores in litter or on fungus covered logs.

Increasing reliance on feeding on fruiting structures of mushrooms selected for the specialized spore brush on the lacinia of gyrophaenines. Members of these early gyrophaenine species were probably not yet totally obligate inhabitants of fresh mushrooms. Mouthpart structure suggest that some members of the "Brachida" lineage may have habits similar to this. This was probably the first adaptive zone occupied by gyrophaenines.

Increasing reliance on hymenium scraping as a feeding mode led to the second adaptive zone of gyrophaenines, obligatory association with fresh mushrooms. This adaptive zone appears to have been reached by the ancestor of the "Sternotropa" plus "Gyrophaena" lineage. Additionally, presence of all members of the "Sternotropa" lineage and some members of the "Gyrophaena" lineage on woody polypores suggests that at this stage the gyrophaenines were limited to woody polypores.

Life cycle adaptations which allowed use of more ephemeral gilled mushrooms were probably important in opening up the final adaptive zone to gyrophaenines, that of gilled fungi. This appears to have been reached only by members of the "Gyrophaena" lineage, particularly *Gyrophaena* and *Phanerota*.

This scenario of major evolutionary trends in gyrophaenines is highly speculative. I provide it here in the hope that it will stimulate additional research to test it. This scenario is particularly sensitive to modification of cladistic relationships among gyrophaenine genera, increased knowledge of the habits of gyrophaenines, particularly members of the "Brachida" lineage and members of the subtribe Bolitocharina, and additional knowledge of distribution of gyrophaenines among mushrooms.

## 6. Prospectus: Future Trends in Research within the Gyrophaenina

Study of evolution of relationships between gyrophaenines and fresh mushrooms provides unique insights into the effect of emphemeral, unpredictable and highly heterogeneous habitats on patterns of evolution within groups which occupy such habitats. At present, this study is in the embryonic stages. Additional study of almost all aspects of gyrophaenine systematics and natural history would be valuable. Particularly useful would be life history and habit information for representative gyrophaenines which live on both soft and woody polypore mushrooms, members of the "Brachida" lineage, members of *Encephalus*, and other closely related aleocharines. It would be very valuable to compare habits and life history of members of other aleocharine groups which are associated with fungi or mushrooms with those of gyrophaenines, especially if hypotheses about the effect of specific habits and habitat can be formulated for comparison. Additional host relationship data would be very useful, particularly if data were gathered rigorously to allow one to distinguish between breeding and feeding hosts and casual visits of adults to mushrooms, and how seasonal, yearly and geographical variation in mushroom flora affects use patterns. Ecological and physiological studies are needed to determine how gyrophaenines find mushrooms, and how they distinguish suitable from unsuitable mushrooms. Nothing is presently known about population dynamics of gyrophaenines and how these affect evolutionary patterns and processes.

The gyrophaenine fauna of most geographical regions is virtually unknown. My experience with the gyrophaenine fauna of Mexico, Central America, and, to a lesser extent, of South America indicates that there are a very large number of undescribed species, and probably undescribed genera, in these areas. It seems likely that the faunas of Africa, Southeast Asia, China, Australia, New Zealand and similar areas are also incompletely described. The fauna of India is probably moderately well described due to the studies of Cameron (1939), but, since he did not provide figures of male genitalia, most of his species are impossible to recognize without reference to types. This is true of most described gyrophaenines. Detailed systematic studies with complete descriptions and illustrations of gyrophaenine faunas of most areas would provide a much needed comparative base.

The heterogeneous assemblage of species presently included in *Gyrophaena* requires study on a world-wide basis. This is a monumental task, but can perhaps be approached by progressive study of increasingly comprehensive monophyletic groups.

Phylogenetic studies are possible at all levels of analysis. Many phylogenetically useful character systems are available and additional study is likely to reveal others. Phylogenetic studies are especially useful if combined with studies of habits and distribution so that hypotheses about evolutionary patterns and processes can be formulated and tested.

The limits of genera described here will probably require modification as the world fauna becomes better known. Also, subsequent analysis of character states in other groups of aleocharines may affect the cladistic hypothesis developed here. This will subsequently affect the hypotheses about evolution of gyrophaenines.

# Literature Cited

Anderson, N.M. 1979. Phylogenetic inference as applied to the study of evolutionary diversification of semi-aquatic bugs (Hemiptera: Gerromorpha). *Systematic Zoology* 28(4):554-578

Arnett, R.H. 1968. *The Beetles of the United States (A Manual for Indentification)*. American Entomological Institute, Ann Arbor, Mich., 1112 pp.

Ashe, J.S. 1981a. Studies of the life history and habits of *Phanerota fasciata* (Say) (Coleoptera: Staphylinidae: Aleocharinae) with notes on the mushroom as a habitat and descriptions of the immature stages. *Coleopterists' Bulletin* 35(1):83-96

Ashe, J.S. 1981b. Pupal cell construction in the Aleocharinae (Staphylinidae). *Coleopterists' Bulletin* 35(3):341-343

Ashe, J.S. (in press). Evidence on the species status of *Panerota fasciata* (Say) and *Phanerota dissimilis* (Erichson) (Staphylinidae: Aleocharinae) from host mushroom relationships. *Coleopterists' Bulletin*

Ashlock, P.D. 1974. The use of cladistics. *Annual Review of Ecology and Systematics* 5:81-99

Ball, G.E. 1975. Pericalina Lebiini: Notes on classification, a synopsis of the New World genera, and a revision of the genus *Phloeoxena* Chaudoir (Coleoptera: Carabidae). *Questiones entomologicae* 11:143-242

Batten, R. 1973. Het boorkomen van *Gyrophaena*-soorten (Col.: Staphylinidae) op Walcheren. *Entomologische Berichten* 33:61-65

Benick, L. 1952. Pilzkäfer und Käferpilze. Ökologische und statistische Untersuchungen. *Acta Zoologica Fennica* 70:1-250

Bernhauer, M. 1916. Neue Staphyliniden des indo-malayischen Faunengebietes, besonders der Philippinen. *Verhandlungen der kaiserlich-königlich zoologisch-botanischen Gesellschaft in Wien* 66:418-431

Bernhauer, M. 1922. Neue Staphyliniden aus Südamerika (23. Beitrag). *Verhandlungen der kaiserlich-königlich zoologisch-botanischen Gesellschaft in Wien* 71:1-23

Bernhauer, M., and Scheerpeltz, O. 1926. *Coleopterorum catalogus. Pars 82, Staphylinidae* 6:499-988

Blackwelder, R.E. 1936. Morphology of the coleopterous family Staphylinidae. *Smithsonian miscellaneous Collections* 94:1-102

Blackwelder, R.E. 1943. Monograph of the West Indian beetles of the family Staphylinidae. *United States National Museum Bulletin* 182:1-658.

Blackwelder, R.E. 1952. The generic names of the beetle family Staphylinidae, with an essay on genotypy. *United States National Museum Bulletin* 200:1-483

Blatchley, W.S. 1910. *An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana.* Nature Publ. Co., Indianapolis, Ind., 1385 pp.

Bock, W.J. 1965. The role of adaptive mechanisms in the origin of higher levels of organization. *Systematic Zoology* 14:272-278

Bock, W.J. 1968. Phylogenetic systematics. *Evolution* 22:646-648

Bonde, N. 1977. Cladistic classification applied to vertebrates. in: M. Hecht, P.C. Goody, and B.M. Hecht (eds.). *Major Patterns in Vertebrate Evolution.* NATO Advanced Study Institute Series. Plenum Press, New York. pp. 741-804

Böving, A.G., and F.C. Craighead. 1930. An illustrated synopsis of the principle larval forms of the order Coleoptera. *Entomologica americana* 11:1-351, 125 pls.

Brundin, L. 1940. Studien über die *Atheta*-Untergattung *Oreostiba* Gangl. *Entomologisk Tidskrift* 18:56-130, 18 pls.

Brundin, L. 1942. Monographie der palaearktischen Arten der *Atheta*-Untergattung *Hygroecia* (Coleoptera: Staphylinidae). *Annales des Naturhistorischen Museums in Wien* 53(2):129-300

Brundin, L. 1943. Zur Kenntnis einiger in die *Atheta*-Untergattung *Metaxya* Muls. und Rey gestellten Arten. *Acta Universitat Lundensis* (N.F.) 54:38 pp., 7 pls.

Brundin, L. 1948. *Microdota*-Studien. *Entomologisk Tidskrift* 69:8-66, 13 pls., 1 fig.

Brundin, L. 1952. *Acrotona*-Studien (Gattung *Atheta*). *Entomologisk Tidskrift* 3:93-145, 78 figs.

Brundin, L. 1954. Die palaearktischen Arten der *Atheta*-Untergattung *Dimetrota* Muls. et Rey. Eine systematische Studie. *Arkiv för Zoologi* 5:369-434, 117 figs.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges, with a monograph of the subfamilies Pondonominae and Aphroteniinae and the austral Heptagyinae. *Svenska Veterskaps Akademien Handlingar* 11:1-472

Brundin, L. 1972. Phylogenetics and biogeography. *Systematic Zoology* 21:69-79

Buxton, P.A. 1960. British Diptera associated with fungi. *Entomologist's Monthly Magazine* 96:61-94

Cameron, M. 1920. New species of Staphylinidae from Singapore. Part III. *Transactions of the Entomological Society of London* (1920):212-284

Cameron, M. 1922. Descriptions of new species of Staphylinidae from the West Indies. *Annual Magazine of Natural History* (Series 9) 9:113-128, 633-652

Cameron, M. 1934. The staphylinid Coleoptera of the New Hebrides. *Stylops* 3:20-24

Cameron, M. 1939. *The fauna of British India, including Ceylon and Burma. Coleoptera.Staphylinidae*, 4, pt.1. 410 pp.

Campbell, J.M. 1969. A revision of the New World Oxyporinae (Coleoptera: Staphylinidae). *Canadian Entomologist* 101(3):225-268

Casey, T.L. 1906. Observations on the staphylinid groups Aleocharinae and Xantholinini, chiefly of America. *Transactions of the Academy of Sciences of Saint Louis* 16:125-434

Casey, T.L. 1911. New American species of Aleocharinae and Myllaeninae. *Memoirs on the Coleoptera* 2:1-259

Cracraft, J. 1974. Phylogenetic models and classification. *Systematic Zoology* 23:71-90

Cracraft, J. 1978. Science, philosophy and systematics. *Systematic Zoology* 27:213-215

Darlington, P.J. 1970. A practical critique of Hennig-Brundin "Phylogenetic Systematics" and Antarctic biogeography. *Systematic Zoology* 19:1-18

De Jong, R. 1980. Some tools for evolutionary and phylogenetic studies. *Zeitschrift fur zoologische Systematik und Evolutionsforschung* 18:1-23

Donisthorpe, H. 1935. The British fungicolous Coleoptera. *Entomologists' Monthly Magazine* 71:21-31

Donisthorpe, H. 1939. *A preliminary list of the Coleoptera of Windsor Forest.* Nathaniel Lloyd & Co., London. 126 pp.

Eichelbaum, F. 1913. Verzeichniss der von mir in den Jahren 1903 und 1904 in Deutsch- und BritischOstafrika eingesammelten Staphylinidae. *Archiv für Naturgeschichte* 79A(3):114-168

Eldrege, N. 1979. Cladism and common sense. In:*Phylogenetic Analysis and Paleontology*, J. Cracraft and N. Eldredge (ed.). Columbia Univeristy Press. New York. pp. 164-198

Eldrege, N., and J. Cracraft. 1980. *Phylogenetic Patterns and the Evolutionary Process*. Columbia University Press, New York. 349 pp.

Elton, C.S. 1966. *The pattern of animal communities.* Methuen, London. 432 pp.

Elton, C.S., and R.S. Miller. 1954. The ecological survey of animal communities with a practical system of classifying habitats by structural characters. *Journal of Ecology* 42:460-496

Erichson, W.F. 1837. *Die Käfer der Mark Brandenburg.* Vol.1,Abt.1. Berlin. 384 pp.

Erichson, W.F. 1839-1840. *Genera et species staphylinorum insectorum coleoptorum familiae* pt.1 (1839) and pt.2 (1840). Berlin. pp. 1-400, 401-954

Fauvel, C.A.A. 1872. *Faune Gallo-Rhénane. Coléoptères.* Caen. 214 pp.

Fauvel, C.A.A. 1875. Faune gallo-rhénane ou species des insectes qui habitant la France, la Belgique, la Hollande, le Luxembourg, la Nassau et la Valais, avec tableaux synoptiques et plances gravées. *Bulletin de la Société linnéenne de la Normandie*, Ser.2, 6:545-738

Fenyes, A. 1918. Coleoptera. Family Staphylinidae, Subfamily Aleocharinae. *Genera Insectorum* 173A:1-110

Fenyes, A. 1918-21. Subfam. Aleocharinae. *Genera Insectorum* 173. Pasadena. 453 pp.

Fenyes, A. 1921. New genera and species of Aleocharinae with a polytomic synopsis of the tribes. *Bulletin of the Museum of Comparative Zoology* 65(2):17-36

Fowler, W.W. 1888. *The Coleoptera of the British Islands. 2.* Ashford, Reeve. London. 444 pp.

Gaffney, E.S. 1979. An introduction to the logic of phylogeny reconstruction. In: *Phylogenetic Analysis and Paleontology*, J. Cracraft and N. Eldredge (ed.). Columbia Univeristy Press. New York. pp. 79-111

Gangelbauer, L. 1895. *Die Käfer von Mitteleuropa. 2.* Vienna. 880 pp.

Graves, R.C. 1960. Ecological observations on the insects and other inhabitants of woody shelf fung (Basidiomycetes: Polyporaceae) in the Chicago area. *Annals of the Entomological Society of America* 53:61-78

Griffiths, G.C.D. 1974. On the foundations of biological systematics. *Acta biotheoretica* 23:85-131

Haeger, E. 1853. Naturgeschichte der *Gyrophaena manea* Erichson (Familie der Staphylinea). *Sitzungsberichte der Akademie der Wissenschaften in Wien* 10:460-464

Hammond, P. 1975. The phylogeny of a remarkable new genus and species of gymnusine staphylinid (Coleoptera) from the Auckland Islands. *Journal of Entomology (B)* 44(2):153-173, 26 figs.

Hansen, V. 1954. *Danmarks Fauna Bd.59. Biller XVII, Rovbiller 3 [Aleocharinae]*. Copenhagen. 499 pp., 31 figs.

Heatwole, H., and A. Heatwole. 1968. Movements, host-fungus preferences, and longevity of *Bolitotherus cornutus* (Coleoptera: Tenebrionidae). *Annals of the Entomological Society of America* 61:18-23

Hecht, M.K., and J.L. Edwards. 1976. The determination of parallel or monophyletic relationships: the proteid salamanders – a test case. *American Naturalist* 110:653

Hecht, M.K., and J.L. Edwards. 1977. The methodology of phylogenetic inference above the species level. In: M.K. Hecht, P.C. Goody, and B.M. Hecht (eds.). *Major patterns in vertebrate evolution*. NATO Advanced Study Institute Series. Plenum Press. New York. pp. 3-51

Hennig, W. 1965. Phylogenetic Systematics. *Annual Review of Entomology* 10:97-116

Hennig, W. 1966. *Phylogenetic Systematics*. University of Illinois Press, Urbana

Herman, L.H. 1972. Revision of *Bledius* and related genera. Part I. The *Aequitorides, Mandibularis* and *Semiferrugineus* groups, and two new genera (Coleoptera; Staphylinidae, Oxytelinae). *Bulletin of the American Museum of Natural History* 149:1-254

Hesler, L.R. 1960. *Mushrooms of the Great Smokies*. University of Tennessee Press. Knoxville. 289 pp.

Hingley, M.R. 1971. The ascomycete fungus, *Daldina concentrica*, as a habitat for animals. *Journal of Animal Ecology* 40(1):17-32

Hoeg, N. 1945. Beitrag zur Systematik der Aleocharinen. Über die Behaarung des Thorax bei der Gattung *Atheta* Thomson. *Entomologiske Meddelelser* 24:264-286

Horrion, A.D. 1967. *Faunistik der Mitteleuropäischen Käfer. Bd.XI: Staphylinidae. 3. Teil: Habrocerinae bis Aleocharinae (Ohne Subtrubus Athetae).* Uberlingen-Bodensee: I-XXIV; 1-419

Hull, D.L. 1970. Contemporary systematic philosophies. *Annual Review of Ecology and Systematics* 1:19-54

Hull, D.L. 1974. *Philosophy of Biological Science.* Prentice-Hall. Englewood Cliffs, N.J. 148 pp.

Hull, D.L. 1979. The limits of cladism. *Systematic Zoology* 28:416-440

Inger, R.F. 1967. The development of frogs. *Evolution* 21:369

Jacquelin du Val, C. 1857-1859. *Genera des Coléoptères d'Europe*. Vol. 2. Paris. 1-40

Kasule, F.K. 1966. The subfamilies of the larvae of Staphylinidae (Coleoptera) with keys to the larvae of teh British genera of Steninae and Proteininae. *Transactions of the Royal Entomological Society of London* 118(8):261-283

Kauffman, C.H. 1971. *The gilled mushrooms (Agaricaceae) of the Michigan and the Great Lakes Region. I & II.* Dover Publications Inc. New York. 924 pp.

Kirby, W. 1832. New genera and species. In: J.F. Stephens. *Illustrations of British Entomology, Mandibulata.* Vol. 5. London. 240 pp.

Kluge, A.G. and J.S. Farris. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18:1-32

Kraatz, G. 1856. *Naturgeschichte den Insecten Deutschlands. Abt. 1, Coleoptera.* Vol. 2, pt. 1-2. Berlin. pp. 1-376

Kraatz, G. 1858. *Naturgeschichte den Insecten Deutschlands. Abt. 1, Coleoptera.* Vol. 2, pt. 5-6. Berlin. pp. 769-1080

Kreiger, L.C. 1967. *The Mushroom Handbook.* Dover Publications Inc. New York. 560 pp.

Lacordaire, J.F. 1854. *Histoire naturelle des insects. General des coléoptères.* Vol. 2. Paris. 548 pp.

Lawrence, J.F. 1973. Host preference in ciid beetles (Coleoptera: Ciidae) inhabiting the fuiting bodies of Basidiomycetes in North America. *Bulletin of the Museum of Comparative Zoology* 145(3):163-212

*Likovsky, Z. 1964. Beiträge zur Kenntin der* Tschechoslowakischen Arten der Gattung *Gyrophaena* Mannerheim (Col: Staphylinidae). *Acta Rerum naturalium Musei nationalis slovenici Bratislava.* 10:51-65

Liles, M. 1956. A study of the life history of the forked fungus beetle, *Bolitotherus cornutus* (Panzer) (Coleoptera: Tenebrionidae). *Ohio Journal of Science* 56:329-337

Lohse, G.A. 1974. *Die Käfer Mitteleuropas. Bd.5. Staphylinidae II (Hypocyphtinae und Aleocharinae), Pselaphidae.* Goeke & Evers. Krefeld. pp. 1-381

Mannerheim, C.G. 1830. Précis d'un nouvel arrangement de la famille des Brachélytres. *Memoirs of the Academy of Sciences of St. Petersburg* 1:413-501

Matthewman, W.G., and D.P. Pielou. 1971. Arthropods inhabiting the sporophores of *Fomes fomentarius* (Polyporaceae) in Gatineau Park, Quebec. *Canadian Entomologist* 103:775-847

Mayr, E. 1974. Cladistic analysis or cladistic classification? *Zeitschrift für zoologische Systematik und Evolutionsforschung* 12:94-128

Mayr, E. 1981. Biological classification: toward a synthesis of opposing methodologies. *Science* 214:510-516

Melsheimer, F.E. 1844. Descriptions of new species of Coleoptera of the United States. *Proceedings of the Academy of Natural Sciences of Philadelphia* 2:26-43

Minch, E.L. 1952. Insect inhabitants of *Polyporus betulinus*. *Journal of the New York Entomological Society. Bulletin* 34:155-157

Mulsant, M.E., and C. Rey. 1871-1875. *Histoire naturelle des coléoptères de France: Brévipennes (Aléochriens).* Vol.1 (1873), Vol.2 (1874), Vol.3 (1873), Vol.4 (1875), Vol 5 (1871)

Mulsant, M.E., and C. Rey. 1872. Tribu des brévipennes: Famille des aléochariens: Huitième Branche: Bolitochares. *Annales de la Société linnéenne de Lyon* (Ser. 2) 19:91-413

Nelson, G.J. 1972. Phylogenetic relationships and classification. *Systematic Zoology* 21:227-231

Nelson, G.J. 1973. Classification as an expression of phylogenetic relationships. *Systematic Zoology* 22:87-91

Pace, A.E. 1967. Life history and behavior of a fungus beetle, *Bolitotherus cornutus* (Tenebrionidae). *Occasional Papers of the Museum of Zoology, University of Michigan* No. 653, 15 pp.

Palm, T. 1968. *Svensk Insectfauna, 9, Skalbaggar. Coleoptera, Kortvingar: Fam. Staphylinidae. Unterfam. Aleocharinae* (Deinopsis – Trichomicra) (5). Stockholm.

Paulian, R. 1941. Les premiers états des Staphylinoidea. *Mémoires du Muséum national d'Histoire naturelle* (NS) 15:1-361

Paviour-Smith, K. 1959. *The ecology of the fauna associated with macrofungi growing on dead and decaying trees.* Unpublished thesis in Bureau of Animal Population Library, Oxford, England

Paviour-Smith, K. 1960a. The fruiting bodies of macrofungi as habitats for beetles of the family Ciidae (Coleoptera). *Oikos* 11(1):43-71

Paviour-Smith, K. 1960b. Insect succession in the "birch-bracket" fungus, *Polyporus betulinus. Proceedings of the International Congress of Entomology 1958* 1:792-796

Paviour-Smith, K. 1964. Habits, headquarters and distribution of *Tetratoma fungorum* F. (Col.: Tetratomidae). *Entomologists' Monthly Magazine* 100:71-80

Paviour-Smith, K. 1965a. Some factors affecting numbers of the fungus beetle *Tetratoma fungorum* F. *Journal of Animal Ecology* 34:700-724

Paviour-Smith, K. 1965b. The life history of *Tetratoma fungorum* F. (Col., Tetratomidae) in relation to habitat requirements, with an account of eggs and larval stages. *Entomologists' monthly Magazine* 100:118-134

Paviour-Smith, K. 1966. Artificial light and *Tetratoma fungorum* F. (Col.: Tetratomidae). *Entomologists' monthly Magazine* 102:56-57

Paviour-Smith, K. 1969. An attempt to correct some mistakes and misconceptions about fungus beetles and their habitats. *Entomologist* 102:86-96

Pescke, K. 1978. Funktionsmorphologische Untersuchungen zur Kopulation von *Aleochara curtula* Goeze (Coleoptera, Staphylinidae). *Zoomorphologie* 89:157-184

Pielou, D.P. 1966. The fauna of *Polyporus betulinus* (Bull.) Fries (Basidiomycetes: Polyporaceae) in Gatineau Park, Quebec. *Canadian Entomologist* 98:1232-1237

Pielou, D.P., and W.G. Matthewman. 1966. The fauna of *Fomes formentarius* (Linn. ex Fries) Kickx. growing on dead birch in Gatineau Park, Quebec. *Canadian Entomologist* 98:1302-1312

Pielou, D.P., and A.N. Verna. 1968. The arthropod fauna associated with the birch bracket fungus, *Polyporus betulinus* in eastern Canada. *Canadian Entomologist* 100:1179-1199

Platnick, N.I. 1977. Cladograms, phylogenetic trees and hypothesis testing. *Systematic Zoology* 26:438-442

Platnick, N.I. 1979. Philosophy and the transformation of cladistics. *Systematic Zoology* 28:537-546

Platnick, N.I., and E. Gaffney. 1977. Systematics: a Popperian perspective. *Systematic Zoology* 26:360-365

Platnick, N.I., and E. Gaffney. 1978. Evolutionary biology: a Popperian perspective. *Systematic Zoology* 27:137-141

Rehfous, M. 1955. Contributions à l'étude des insectes des champignons. *Mitteilungen der schweizerische entomologische Gesellschaft* 28:1-106

Reitter, E. 1909. *Fauna Germanica. Die Käfer des deutschen Reiches*. Vol. 2. Stuttgart. 220 pp.

Reitter, E. 1918. *Fauna Germanica. Die Käfer des deutschen Reiches*. Vol.5. Stuttgart. 343 pp.

Rey, C. 1886. Larve de la *Gyrophaena affinis* Sahlb. *Annales de la Société linnéenne de Lyon* 33:163-165

Ross, H.H. 1974. *Biological Systematics*. Addison-Wesley Co., Inc. Reading, Mass. 345 pp.

Saether, O.A. 1979. Underlying synapomorphies and anagenetic analysis. *Zoologica scripta* 8:305-312

Sawada, K. 1970. Aleocharinae (Staphylinidae, Coleoptera) of the IBP-station in the Shiga Heights, central Japan (I). *Bulletin of the National Sciences Museum* 13(1):21-64

Sawada, K. 1972. Methodological research in the taxonomy of Aleocharinae. *Contributions of the Biological Laboratory of Kyoto University* 24(1):31-59

Sawada, K. 1974. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). I. Amidobia. *Contribution of the Biological Laboratory of Kyoto University* 24(3):145-186

Sawada, K. 1977. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). III. Japanese species described by previous authors. *Contribution of the Biological Laboratory of Kyoto University* 25(2):171-222, 22 figs.

Schaeffer, B., M.K. Hecht, and N. Eldredge. 1972. Paleontology and phylogeny. *Evolutionary Biology* 6:31-46

Scheerpeltz, O. 1930. *Käfer (Coleoptera). Tierwelt Mitteleuropas. Insecten 2.* 12:1-272

Scheerpeltz, O. 1934. *Coleopterum catalogus. Pars 130, Staphylinidae. VII. Supplementum II.* Berlin. pp. 1501-1881

Scheerpeltz, O., and K. Höfler. 1948. *Käfer and Pilze.* Verlag für Jugend und Volk. Vienna. 351 pp., 9 pls.

Schubert, K. 1908. Beitrag zur Staphylinidenfauna Ostindiens (West-Himalaya). *Deutsche entomologische Zeitschrift* 1908:603-625

Seevers, C.H. 1951. A revision of the North American and European staphylinid beetles of the subtribe Gyrophaenae (Aleocharinae: Bolitocharini). *Fieldiana: Zoology* 32:659-762

Seevers, C.H. 1957. A monograph on the termitophilous Staphylinidae (Coleoptera). *Fieldiana: Zoology* 40:1-334

Seevers, C.H. 1965. The systematics, evolution and zoogeography of staphylinid beetles associated with army ants (Coleoptera, Staphylinidae). *Fieldiana: Zoology* 47:1-351

Seevers, C.H. 1978. A generic and tribal revision of the North American Aleocharinae (Coleoptera, Staphylinidae). *Fieldiana: Zoology* 71:1-289

Sharp, D. 1876. Contributions to an insect fauna fo the Amazon Valley: Coleoptera – Staphylinidae. *Transactions of the entomological Society of London* 1876:27-208

Sharp, D. 1883-1887. *Biologia Centrali-Americana: Insecta, Coleoptera. 1. (pt.2).* London. pp. 145-312, pl. 6-7 (1883); pp. 313-392, pl. 8-9 (1884); pp. 393-536, pl. 10-13 (1885); pp. 537-672, pl. 14-16 (1886); pp. 673-824, pl. 17-19 (1887).

Simpson, G.G. 1953. *The major features of evolution.* Columbia University Press. New York. 434 pp.

Simpson, G.G. 1975. Recent advances in methods of phylogenetic inference. In: W.P. Luckett and F.S. Szalay (eds.). *Phylogeny of the Primates.* Plenum Press. New York. pp. 3-19

Smith, A.H. 1958. *The Mushroom Hunters Guide.* University of Michigan Press. Ann Arbor. 197 pp.

Smith, H.V., and A.H. Smith. 1973. *How to know the non-gilled fleshy fungi.* Wm.C. Brown Co. Dubuque, Iowa. 402 pp.

Smith, A.H., H.V. Smith and N.S. Weber. 1979. *How to know the gilled mushrooms.* Wm.C. Brown Co. Dubuque, Iowa. 334 pp.

Stephens, J.F. 1832. *Illustrations of British Entomology, Mandibulata.* Vol. 5. London. 240 pp.

Thompson, C.G. 1860. *Skandinaviens Coleoptera.* Vol. 2. Lund. 304 pp.

Thompson, C.G. 1867. Entomologiska anteckningen under en resa i Skåne 1866. *Öfversigt af kongl. Svenska Veterskap Akademiens Förhandlingar* 24:39-52

Watrous, L.E., and Q.D. Wheeler. 1981. The out-group comparison method of character analysis. *Systematic Zoology* 30:1-11

Weiss, H.B. 1920a. Coleoptera associated with *Polyporus versicolor* L. in New Jersey. *Psyche* 27:137-139

Weiss, H.B. 1920b. The insect enemies of polyporid fungi. *The American Naturalist* 54:443-447

Weiss, H.B. 1920c. Notes on the fungus beetle, *Cis vitula* Mann. *Psyche* 27:133-134

Weiss, H.B., and E. West. 1920. Fungus insects and their hosts. *Proceedings of the Biological Society of Washington* 31:236-237

Weiss, H.B., and E. West. 1921. Additional notes on fungus insects. *Proceedings of the Biological Society of Washington* 34:167-172

Welch, R.C. 1964. *The biology of the genus* Aleochara *Grav. (Coleoptera, Staphylinidae)*. Unpublished thesis. University of London. 432 pp.

Westwood, J.O. 1838. *An introduction to the modern classification of insects*. Vol. 2. London. pp. 1-48

White, I.M. 1975. *Studies in the Aleocharine genus Gyrophaena* Mannerheim (Coleoptera: Staphylinidae). B.Sc. Thesis. University of London.

White, I.M. 1977. The larvae of some British species of *Gyrophaena* Mannerheim (Coleoptera: Staphylinidae) with notes on the taxonomy and biology of the genus. *Biological Journal of the Linnean Society of London* 8:297-317

Wiley, E.O. 1975. Karl R. Popper, systematics, and classification: A reply to Walter Bock and other evolutionary taxonomists. *Systematic Zoology* 24:233-242

Wiley, E.O. 1981. *Phylogenetics. The Theory and Practice of Phylogenetic Systematics*. John Wiley and Sons, N.Y.

Wilson, E.O. 1965. A consistency test for phylogenics based on contemporaneous species. *Systematic Zoology* 14:214

Wüsthoff, W. 1937. Beitrag zur Kenntnis der europäischen Arten der Gattung *Gyrophaena*. *Decheniana* 95B:137-146, 12 pls.

Yosii, R., and K. Sawada. 1976. Studies on the genus *Atheta* Thomson and its allies (Coleoptera, Staphylinidae). II: Diagnostic characters of genera and subgenera with description of representative species. *Contribution of the Biological Laboratory of Kyoto University* 25:11-140, 59 figs.

**Table 1:** Plesiotypic and apotypic states of characters discussed in text (letters in parentheses are character state designations used in text).

| Character | Plesiotypic | Apotypic |
|---|---|---|
| 1 **Body setae:** microsetae | –numerous, more or less short, densely and uniformly distributed over body (A) | –more or less long and silky, densely and uniformly distributed (B)<br>–short, number reduced, body subglabrous ($C_1$)<br>–short, number very reduced, body more or less glabrous ($C_2$) |
| 2 **Body setae:** macrosetae | –small, difficult to distinguish from microsetae (A) | –larger, easily distinguished from microsetae ($B_1$)<br>–extremely large, very conspicuous ($B_2$) |
| 3 **Sculpture** | –uniformly reticulate (A) | –obsolete or smooth on one or more body parts ($B_1$)<br>–absent, body integument uniformly smooth ($B_2$) |
| 4 **Head:** medial macrosetae | –pair of macrosetae present medially on vertex (A) | –macrosetae absent on vertex (B) |
| 5 **Head:** Infraorbital carina | –well developed, complete ventrally (A) | –incomplete, reduced or absent ventrally (B) |
| 6 **Head:** lateral macrosetae | –lateral macrosetae absent (A) | –2 lateral macrosetae on each side of dorsal surface of head (B) |
| 7 **Eyes** | –size moderate (A) | –extremely large, prominent (B) |
| 8 **Antenna:** article 4 | –similar in setation and general shape to articles 5–10 (A) | –similar in setation and general shape to articles 1–3 (B) |

*cont. next page*

*Table 1 cont.*

| Character | Plesiotypic | Apotypic |
|---|---|---|
| 9 **Labrum:** number of setae | –numerous setae in addition to basic setal pattern (A) | –few or no setae in addition to basic setal pattern (B) |
| 10 **Labrum:** $\alpha$–sensillum | –filiform, seta-like (A) | –thickened, hyaline (B) |
| 11 **Labrum:** $\epsilon$–sensillum | –large, indistinguishable from labral setae (A) | –setose but much smaller than labral setae ($B_1$)<br>–reduced, small, peg-like ($B_2$) |
| 12 **Labrum:** lateral sensilla row (position) | –sensilla near or at lateral margin of labrum (A) | –sensilla more or less distant from lateral margin of labrum (B) |
| 13 **Labrum:** lateral sensilla row (development) | –4 or 5 well developed sensilla (A) | –number and development of sensilla reduced (B) |
| 14 **Labrum:** A.L.1 and A.L.2 | –origin more or less distant from margin of labrum (A) | –origin at margin of labrum (B) |
| 15 **Labrum:** internal setose areas | –densely setose area present internally on each side of labrum (A) | –densely setose area absent internally on each side of labrum (B) |
| 16 **Mandibles:** form of apex | –not bifid at apex (A) | –left mandible bifid at apex (B)<br>–both mandibles bifid at apex (C) |
| 17 **Mandibles:** internal tooth | –right mandible with well developed internal tooth (A) | –mandibles without well developed internal tooth (B)<br>–both mandibles with well developed internal tooth (C) |
| 18 **Lacinia:** form of apex | –more or less acute (A) | –obliquely truncate (B) |
| 19 **Lacinia:** apical teeth | –relatively few, in a loosely defined patch, slightly, or not at all differentiated from lateral spines or teeth (A) | –numerous, closely spaced, in well defined patch, well differentiated from lateral spines or teeth (B) |

*cont. next page*

*Table 1 cont.*

| | Character | Plesiotypic | Apotypic |
|---|---|---|---|
| 20 | **Lacinia:** inner face (teeth) | –numerous, densely arranged, often spine-like teeth present (A) | –few, more or less scattered teeth present ($B_1$)<br>–teeth absent ($B_2$) |
| 21 | **Lacinia:** inner face (setae) | –very numerous, densely arranged, irregularly scattered (A) | –less numerous, few to many, more or less loosely and irregularly scattered ($B_1$)<br>–few to many in a well differentiated vertical row ($B_2$) |
| 22 | **Galea:** apical setae (arrangement) | –numerous, in close numerous rows (8–10 or more) (A) | –numerous, rows fewer, (5–8), but not close ($B_1$)<br>–less numerous, in 4 well separated rows ($B_2$) |
| 23 | **Galea:** apical setae (structure) | –long, filiform, setose (A) | –flattened, subspatulate or plate-like (B) |
| 24 | **Labium:** form of ligula | –elongate, bifid at apex (inferred) (A) | –short, entire, protruded and parallel sided (B)<br>–short, entire, broadly rounded (C)<br>–short, protruding, parallel sided, divided 1/2 to 1/3 distance to base ($D_1$)<br>–short, protruding, parallel sided, divided almost or fully to base ($D_2$)<br>–elongate, parallel sided, divided in anterior 1/3 (E) |
| 25 | **Labium:** number of medial setae | –2 medial setae (A) | –1 medial seta ($B_1$)<br>–medial setae absent ($B_2$) |
| 26 | **Pronotum:** hind margin (sinuosity) | –markedly bisinuate (A) | –slightly binsinuate ($B_1$)<br>–not bisinuate ($B_2$) |

cont. next page

*Table 1 cont.*

| | Character | Plesiotypic | Apotypic |
|---|---|---|---|
| 27 | **Pronotum:** hind margin (emargination) | –without medial emargination (A) | –with medial emargination (B) |
| 28 | **Pronotum:** shape | –markedly transverse (A) | –broadly oval ($B_1$)<br>–more or less subquadrate ($B_2$) |
| 29 | **Pronotum:** lateral borders | –moderately to slightly deflexed (A) | –not at all or very slightly deflexed (B)<br>–very markedly deflexed (C) |
| 30 | **Hypomeron:** visiblity | –not visible in lateral view (A) | –narrowly visible in lateral view ($B_1$)<br>–broadly or in large part visible in lateral view ($B_2$) |
| 31 | **Scutellum:** visibility | –visible in dorsal view (A) | –hidden in dorsal view (B) |
| 32 | **Elytron:** latero-apical angle | –markedly or deeply sinuate (A) | –slightly or shallowly sinuate ($B_1$)<br>–rectilinear, not at all sinuate ($B_2$) |
| 33 | **Prosternum:** shape | –markedly transverse (A) | –slightly to moderately transverse (B) |
| 34 | **Prosternum:** medial ornamentation | –tooth, carina or knob medially (A) | –tooth, carina or knob absent (B)<br>–transverse carina ($C_1$)<br>–transverse carina absent ($C_2$) |
| 35 | **Mesosternum:** carina (development) | –well developed medial carina from anterior margin to apex of metasternal process (A) | –medial carina more or less reduced, not complete to end of mesosternal process (B)<br>–medial carina modified to low, diffuse, broad ridge (C)<br>–carina absent (D) |

*cont. next page*

*Table 1 cont.*

| Character | Plesiotypic | Apotypic |
|---|---|---|
| 36 **Intercoxal processes:** relative lengths | –mesosternal process reaching to middle or slightly beyond middle of mesocoxal cavities (A) | –mesosternal process attaining or almost attaining posterior margin of mesocoxal cavities (B) |
| 37 **Intercoxal processes:** separation | –processes more or less separated, isthmus present (A) | –processes contiguous, isthmus absent (B) |
| 38 **Intercoxal processes:** juncture | –truncate or broadly rounded, with a distinct suture (A) | –fused, suture invisible (B) |
| 39 **Metepisternal setae** | –numerous, uniformly and irregularly distributed (A) | –numerous, in 2 irregular rows ($B_1$)<br>–in a single well differentiated row ($B_2$)<br>–setae absent or very few, restricted to posterior 1/3 or less (C) |
| 40 **Metepisternum:** carina | –setose area not delimited anteriorly and ventrally by a carina (A) | –setose area delimited anteriorly and ventrally by a slightly to moderately developed carina (B) |
| 41 **Abdomen:** number of transversely impressed tergites | –3–6 moderately markedly transversely impressed (A) | –slightly impressed, one or more of 3–5 without impressions ($B_1$)<br>–all tergites without transverse impressions ($B_2$) |
| 42 **Tergum 10:** medial setose area | –more or less quadrate, with numerous setae (A) | –more or less quadrate, with fewer, more widely scattered setae (B)<br>–chevron-shaped, with numerous setae not in distinct rows ($C_1$)<br>–chevron-shaped, with setae in 1 or 2 well developed rows ($C_2$)<br>–V-shaped, few setae in 1 or 2 well developed rows (D) |

*cont. next page*

*Table 1 cont.*

| Character | Plesiotypic | Apotypic |
|---|---|---|
| 43 **Tergum 10:** medial setae (structure) | –more or less long, setiform, unmodified (A) | –more or less short and stubby, setiform ($B_1$)<br>–flattened, more or less subspatulate ($B_2$) |
| 44 **Spermatheca:** latero-apical plate | –latero-apical plate absent (A) | –latero-apical plate present (B) |
| 45 **Spermatheca:** modification | –simple, without elongate neck (A) | –neck elongate distal to latero-apical plate (B)<br>–neck elongate proximal to latero-apical plate (C) |
| 46 **Aedeagus:** median lobe | –apical process simple, lobe-like; flagellum short, unsclerotized, tube-like (A) | –apical process elongate, very slender, blade-like, asymmetrical or highly complex; flagellum very slender, elongate, whip-like or complex and more or less sclerotized (B) |
| 47 **Aedeagus:** parameres | –apical lobe of paramerites symmetrical, simple, elongate, with 4 more or less equal setae near apex (A) | –apical lobe of paramerites asymmetrical or very elongate, with setae very unequal and not all near apex (B) |

TABLE 2

Distribution of plesiotypic and apotypic character states among gyrophaenine genera

| Character | Bolitocharini | Probrachida | Brachida | Agaricochara | Agaricomorpha | Brachychara | Adelarthra | Sternotropa | Pseudoligeta | Neobrachida | Gyrophaena | Phanerota | Eumicrota | Encephalus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 1 Body setae: microsetae | A, $C_1$ | B | $B_1$, $C_1$ | A | A | $C_1$ | $C_1$ | A $C_1$ | A, $C_1$ | $C_1$ | A, $C_1$, $C_1$ | $C_1$, $C_1$ | A | $C_1$ |
| 2 Body setae: macrosetae | A | A, $B_1$ | A, $B_1$ | A | A | A, $B_1$ | $B_1$ | A, $B_1$ | A | $B_1$ | $B_1$ | $B_1$ | A, $B_1$ | A, $B_1$ |
| 3 Sculpture | A | A, $B_1$ | A | A | A, $B_1$ | $B_1$ | $B_1$ | A, $B_1$, $B_1$ | A, $B_1$ | $B_1$ | A, $B_1$, $B_1$ | A, $B_1$, $B_1$ | A, $B_1$ | A |
| 4 Head: medial macrosetae | B | B | A | B | B | (a) | B | B | B | B | B, A | B | B, A | B |
| 5 Head: infraorbital carina | A | A | A | A | A | A | A | A, B | B | A | A | A | A | A |
| 6 Head: lateral macrosetae | A | A | A | A | A | A | A | A | A | A | A | A, B | A | A |
| 7 Eyes | A | A | A | A | A | A | A | A | A | A | A | B | A | A |
| 8 Antenna: article 4 | A, B | A | A, B | B | B | B | B | B | B | B | B | B | B | B |
| 9 Labrum: number of setae | A | A, B | A, B | B | B | B | B | B | B | ? | B | B | B | B |
| 10 Labrum: α sensillum | A, B | A, B | B | A | A | A | A | A | A, B | ? | A | A | A | B |
| 11 Labrum: ε sensillum | $B_1$ | A, $B_1$, $B_1$ | A, $B_1$, $B_1$ | $B_1$ | $B_1$, $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$, $B_1$ | ? | $B_1$, $B_1$ | $B_1$ | $B_1$ | $B_1$, $B_1$ |
| 12 Labrum: lateral sensilla (position) | A, B | A | A | B | B | A | A | A | – | ? | B | B | B | B |
| 13 Labrum: lateral sensilla (dvlpmnt) | A, B | A | A, B | A | A | A | B | B, A | B | ? | A, B | A | A | B |
| 14 Labrum: AL1 and AL2 | A | A | A | B | B | B | B | B | B | ? | B | B | B | A |
| 15 Labrum: internal setose areas | ? | A | A, B | B | B | B | B | B | B | ? | B | B | B | B |
| 16 Mandibles: form of apex | A | A, B, C | B | A | A | A | A | A | A | A | A | A | A | A |
| 17 Mandibles: internal tooth | A | A, B | A | A | A | A | A | A | A, B | ? | A | A | A | A |
| 18 Lacinia: form of apex | A | B | B | B | B | B | B | B | B | B | B | B | B | B |
| 19 Lacinia: apical teeth | A | B | B | B | B | B | B | B | B | B | B | B | B | B |
| 20 Lacinia: inner face (teeth) | A | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ |
| 21 Lacinia: inner face (setae) | A | A, $B_1$ | A, $B_1$ | $B_1$ | $B_1$, $B_1$ | $B_1$ | $B_1$ | $B_1$, $B_1$ | $B_1$ | ? | $B_1$ | $B_1$ | $B_1$ | $B_1$ |
| 22 Galea: apical setae (arrngmnt) | A | A, $B_1$ | $B_1$, $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | ? | $B_1$ | $B_1$ | $B_1$ | $B_1$ |
| 23 Galea: apical setae (struct) | A | A | A, B | B | B | B | B | B | B | B | B | B | B | B |
| 24 Labium: form of ligula | A | C | C | $D_1$ | $D_1$ | $D_1$ | $D_1$ | $D_1$ | $D_1$ | E | B | B | B | C |

cont. next page

TABLE 2 continued

| Character | Bolitocharini | Probrachida | Brachida | Agaricochara | Agaricomorpha | Brachychara | Adelarthra | Stenotrops | Pseudoligota | Neobrachida | Gyrophaena | Phanerota | Eumicrota | Encephalus |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 25 Labium: number of medial setae | A, B | A | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$ | $B_1$, $B_2$ | $B_1$ | $B_1$ | $B_1$, $B_2$ | $B_1$, $B_2$ | $B_1$ | $B_1$ |
| 26 Pronotum: hind margin (sinuosity) | $B_2$ | $B_2$ | $B_2$ | $B_1$ | A, $B_1$ | A | A | A | $B_1$ | $B_1$ | $B_1$, $B_2$ | $B_2$ | A, $B_1$ | $B_2$ |
| 27 Pronotum: hind margin (emarg) | A | B | A | A | A | A | A | A | A | A | A, B | A | A | B |
| 28 Pronotum: shape | $B_1$, $B_2$ | $B_1$, $B_2$ | $B_1$, $B_2$ | $B_1$ | A | A | A | A | A | A | $B_1$, $B_2$ | $B_1$ | A, B | A |
| 29 Pronotum: lateral borders | B | A | A | B | A | C | C | A | A | A | A, B | B | A, B | C |
| 30 Hypomeron: visiblity | B | A | A | B | A | A | A | A | A | A | A, B | B | A, B | A |
| 31 Scutellum: visibility | A | A | A | A | A | B | B | A, B | B | A | A | A | A | A |
| 32 Elytron: latero-apical angle | A | $B_2$ | $B_2$ | $B_1$ | A | A | A | A | A, $B_1$ | A | $B_1$, $B_2$ | $B_2$ | A, $B_1$ | $B_2$ |
| 33 Prosternum: shape | A, B | B | B | A, B | A | A | A | A | A | A | B | B | A | A |
| 34 Prosternum: medial ornamentation | A | $C_1$ | $C_1$ | $C_1$ | A | A | A | A | A | A | B, $C_1$, $C_2$ | B, $C_1$, $C_2$ | B | $C_1$ |
| 35 Mesosternum: carina (dvlpmnt) | A, B | A, D | C, D | B | A, B | C | A | A, B | D | C | D | D | D | C |
| 36 Intercoxal processes: rel lengths | A | B | B | A | A | A | ? | A | ? | A | A, B | A | A | B |
| 37 Intercoxal processes: separation | A, B | B | B | A | B | B | B | B | B | B | B | B | B | B |
| 38 Intercoxal processes: juncture | –, A | A | A | – | A, B | B | B | A, B | B | A | A, B | A | A, B | A |
| 39 Metepisternal setae | A, B | A | A, $B_1$, $B_2$ | $B_2$ | $B_1$, $B_2$ | $B_1$ | C | $B_1$ | B, C | B | $B_2$ | $B_2$ | $B_2$ | C |
| 40 Metepisternum: carina | A, B | A | A | B | A, B | A | A | A | A | A | A, B | A, B | A | A, B |
| 41 Abdomen: # trnsv impress terga | A | A | A | A | A, $B_1$ | $B_1$ | A | A, $B_1$ | $B_1$, $B_2$ | A | A | A | A | $B_1$ |
| 42 Tergum 10: medial setose area | C | A | A | A | $C_1$ | $C_2$ | B | $C_1$, $C_2$ | B | $C_2$ | A, B | A, B | D | A, B |
| 43 Tergum 10: medial setae (form) | A | A | A | $B_1$ | $B_2$ | $B_2$ | $B_1$ | $B_2$ | $B_1$ | $B_2$ | $B_2$ | $B_2$ | $B_2$ | ?$B_1$ |
| 44 Spermatheca: latero-apical plate | A | B | B | B | B | B | B | B | B | B | B | B | B | B |
| 45 Spermatheca: modification | – | C | B | A | A | A | ? | A | A | A | A C | C | A | A |
| 46 Aedeagus: median lobe | A | B | B | B | B | B | B | B | B | ? | A, B | B | B | A |
| 47 Aedeagus: parameres | A | A | A | A, B | A | A | B | B | B | ? | A, B | A | A, B | A |

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## TABLE 3

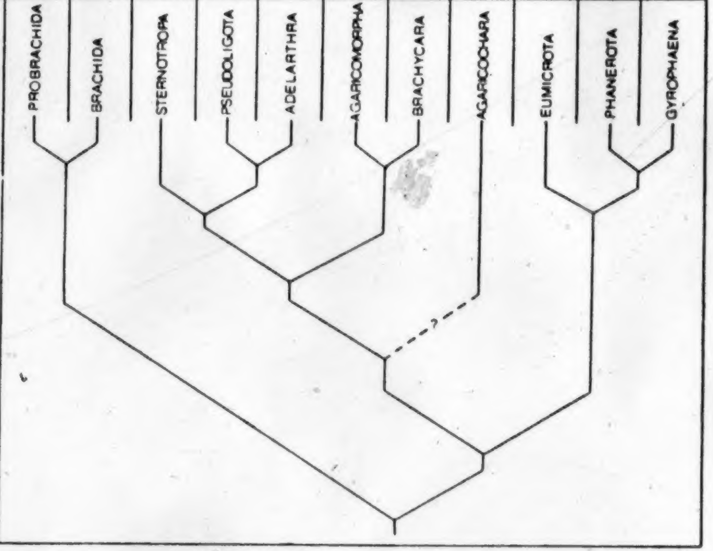
## GENERAL CHARACTERISTICS OF POLYPORE AND GILLED MUSHROOMS AS HABITATS FOR GYROPHAENINES

| | Polypores | Gilled |
|---|---|---|
| 1)Persistence | relatively long lived | short to very short lived |
| 2)Spore Production | inside tubes | on surface of "gills" |
| 3)Length of Spore Production | often sporadically over a long period | numerous spores produced over a short period. |

### TABLE 4

Generalized distribution of members of gyrophaenine genera among major mushroom groups

| | PROBRACHIDA | BRACHIDA | STERNOTROPA | PSEUDOLIGOTA | ADELARTHRA | AGARICOMORPHA | BRACHYCARA | AGARICOCHARA | EUMICROTA | PHANEROTA | GYROPHAENA |
|---|---|---|---|---|---|---|---|---|---|---|---|
| UNKNOWN | ++++ | +++ | | | | | | | | | |
| BOLETES | | | | | | | | | +− | | +− |
| GILLED MUSHROOMS | | | | | | | | | +− | +++ | ++++ |
| PERSISTENT GILLED MUSHROOMS usually stemless on logs | | | | | | | | | ++ | +++ | ++ |
| FLESHY POLYPORES | | +? | | | | ++ | | | +++ | +− | + |
| WOODY POLYPORES | | +? | ?? | ++++ | ? | ++++ | ++++ | ++++ | ++ | | + |
| RESUPINATE POLYPORES | | | ? | ? | | + | + | + | + | | |



++++) very abundant

+++) abundant

++) common

+) rare

+−) occasional

## TABLE 5

Generalized distribution of North American members of major species groups of Gyrophaena and Phanerota among members of commonly encountered gilled mushroom families

| spore color | white | | | | | pink | light brown | chocolate brown | grey black |
|---|---|---|---|---|---|---|---|---|---|
| beetle taxon / mushroom taxon | AMANITACEAE | LEPIOTACEAE | HYGROPORACEAE | RUSSULACEAE | TRICHOLOMATACEAE | RHODOPHYLLACEAE | CORTINARIACEAE | AGARICACEAE | COPRINACEAE |
| **GYROPHAENA** (spp. grps.) | | | | | | | | | |
| NANA grp. | | | | | | | ++++ | | |
| KEENI grp. | + | | | | + | | +++ | | |
| LAETULA grp. | + | | | + | ++ | | | | |
| EGENA grp. | | | | ++++ | | | | | |
| AFFINIS grp. | ++ | | | | +++ | | | | |
| CONICIVENTRIS grp. | + | | | | +++ | | + | | |
| PULCHELLA grp. | + | | | + | +++ | | + | | |
| BIHAMATA grp. | ++ | | | | ++ | | ++ | | |
| **PHANEROTA** spp. | + | | | +++ | ++ | | | | |

++++) very abundant
+++) abundant
++) common
+) rare

## Table 6

Summary of host records for Phanerota fasciata (Say)

| Mushroom Taxon | Total No. Collections | Total Specimens Collected |
|---|---|---|
| [1]Amanita spp. | 11 | 83 |
| Amanitopsis sp. | 1 | 50 |
| [2]Clitocybe illudens | 3 | 61 |
| Lactarius spp. | 12 | 394 |
| Russula spp. | 22 | 329 |
| Others (6 genera)[3] | 12 | 41 |

[1] Most specimens from 2 collections from A. solitaria (Bull. ex Fr.) (55 specimens), and 1 collection from A. verna (Fr.) Quel. (24 specimens).

[2] Most specimens from 1 collection (52 specimens).

[3] Armillaria (2 coll.), Boletus (2 coll.), Clitocybe (2 coll.), Entoloma (1 coll.), Lepiota (1 coll.), Pleurotus (4 coll.).

## Table 7

Host records for *Gyrophaena nanoides* Seev.

| Mushroom Taxon | Number Collections | Total Specimens Collected |
|---|---|---|
| *Amanita verna* | 1 | 5 |
| *Amanita* sp. | 1 | 3 |
| *Clitocybe clavipes* | 1 | 2 |
| *Clitopilus* sp. | 1 | 1 |
| *Collybia confluens* | 1 | 1 |
| *Cortinarius* spp. | 2 | 63 |
| *Mycena* sp. | 1 | 1 |
| *Pleurotus* sp. | 1 | 3 |
| *Russula crustosa* | 1 | 1 |
| *Tricholoma* sp. | 1 | 1 |

## Table 8

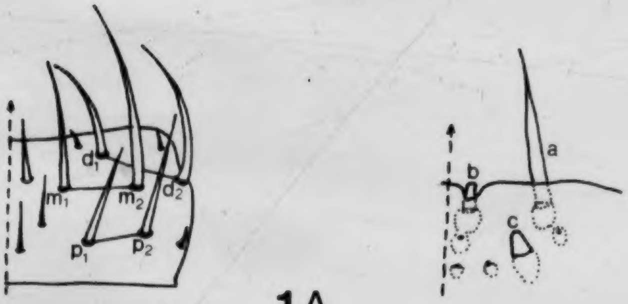
Summary of host records for Gyrophaena monticola Seev.

| Mushroom Taxon | Number Collections | Total Specimens Collected |
|---|---|---|
| Cortinarius spp. | 11 | 336 |
| Crepidotus spp. | 4 | 124 |
| Gymnopilus spp. | 3 | 83 |
| Pholiota squarrosa | 2 | 113 |
| Pleurotus ostreatus | 1 | 137 |
| all other mushrooms (5 genera)* | 5 | 35 |

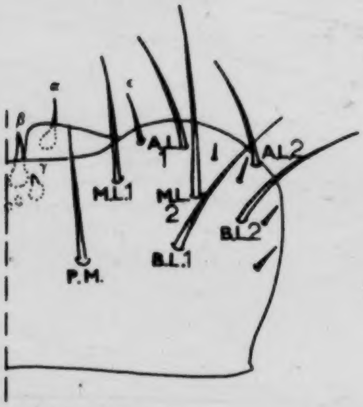
* Clitocybe (1 Coll.); Undet. Cortinariaceae (2 Coll.); Undet. Tricholomataceae (2 Coll.).

Figure 1. Terms for major setae and sensilla of labrum of adult aleocharines discussed in this study. A) Terms after Sawada (1972) (redrawn from Sawada (1972); B) Terms proposed in this study (A.L.= apical lateral; B.L.= basal lateral; M.L.= medial lateral; P.M.= paramedial).

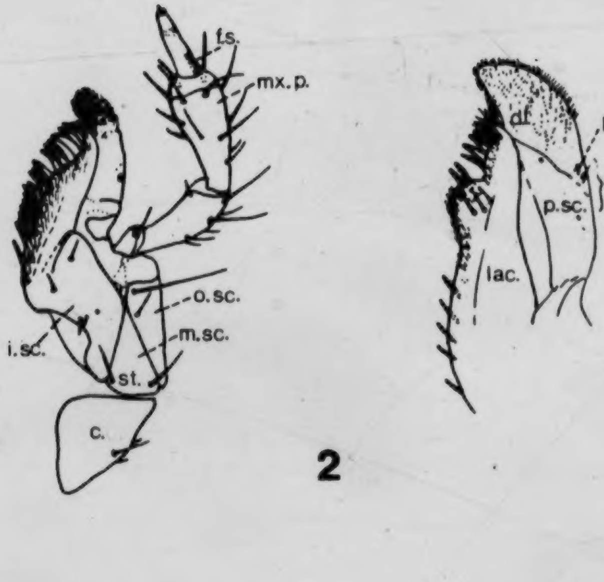
Figure 2. Terms for structures on maxilla of adult aleocharines discussed in the text, dorsal aspect. (redrawn and simplified from Sawada, 1971). (b.s.= basal sensillum; c.= cardo; d.l.= distal lobe; f.s.= filamentous sensillum; gal.= galea; i. sc.= inner sclerite; lac.=lacinia; m.sc.= medial sclerite; mx.p.= maxillary palpus; o.sc.= outer sclerite; p.sc.= proximal sclerite; st.= stipes).


$d_1$
$m_1$
$m_2$
$d_2$
$p_1$
$p_2$
a
b
c

**1A**


α
ε
β
γ
A.L. 1
A.L.2
M.L.1
M.L. 2
B.L.1
B.L.2
P.M.

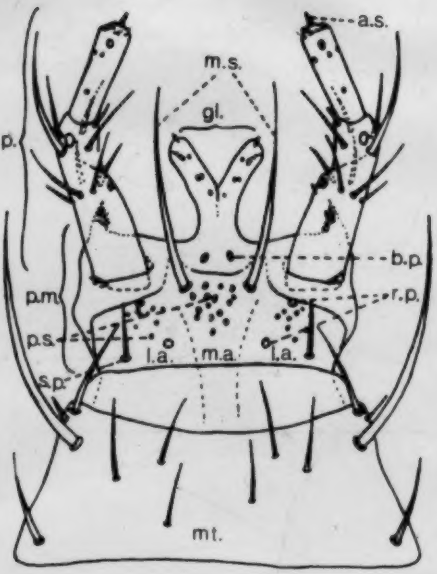
**1B**


f.s.
mx.p.
o.sc.
m.sc.
i.sc.
st.
c.
d.f.
b.s.
gal.
p.sc.
lac.

**2**

Figure 3. Terms for structures on labium of adult aleocharines discussed in the text (redrawn and slightly simplified from Sawada, 1972) (a.s.= apical spine; b.p.= basal pore; gl.= glossae; l.a.= lateral area; l.p.= labial palpus; m.a.= medial area; m.s.= medial setae; mt.= mentum; p.m.= prementum; p.s.= pseudopores; r.p.= real pores).

Figure 4. Generalized position and terms for macrosetae on the pronotum of adult Gyrophaenina (L = laterals; ML = mesolaterals; PM = paramedial; M = medials).


a.s.
m.s.
gl.
l.p.
b.p.
p.m.
r.p.
p.s.
l.a.
m.a.
l.a.
s.p.
mt.

3

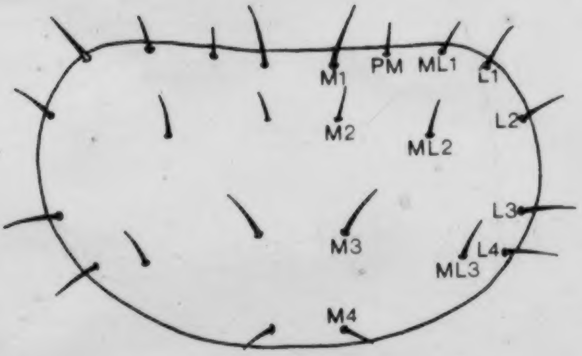

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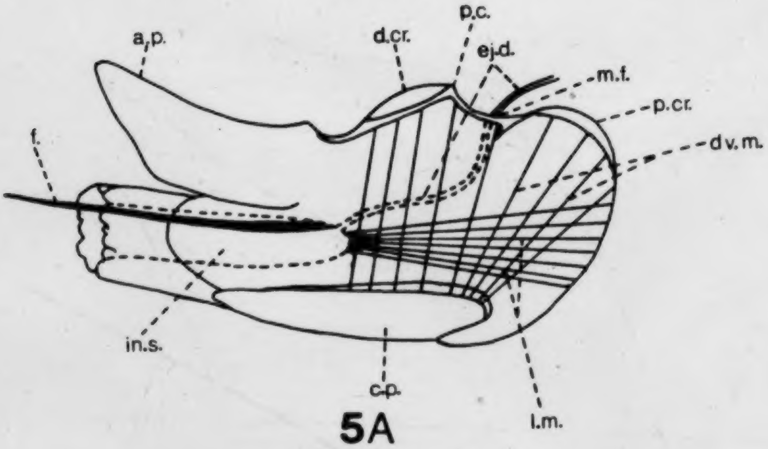
Figure 5. Terms for structures on the median lobe of the aedeagus. A) Generalized aleocharine median lobe. B) Generalized gyrophaenine median lobe. (a.p.= apical process; c.p.= compressor plate; d.cr.= distal crest; dv.m.= dorso-ventral muscles; ej.d.= ejaculatory duct; f.= flagellum; in.s.= internal sac; l.m.= longitudinal muscles; m.f.= medial foramen; p.c.= paramere condyles; p.cr.= proximal crest).

Figure 6. Terms for structures on parameres of the aedeagus of adult aleocharines discussed on this study. (con.= condylite; par.= paramerite; ap.l.= apical lobe of paramerite; h.z.= hinge zone; v.s.= velar sac).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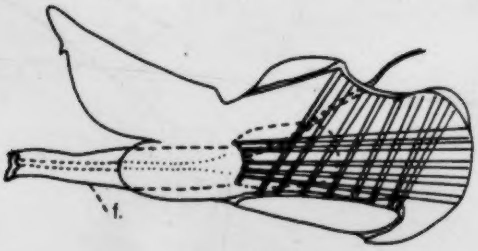
5A



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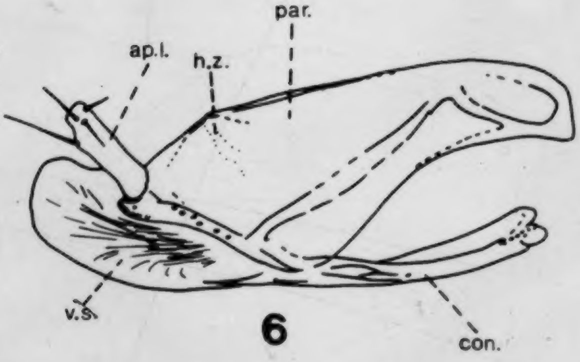
ap.l.
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par.
v.s.
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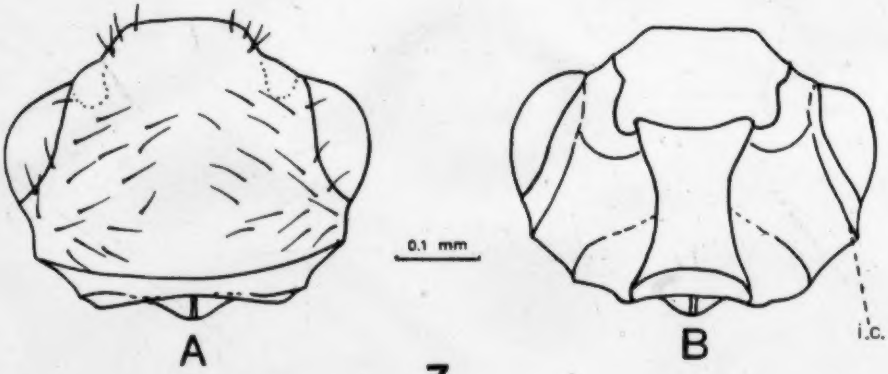
6

Figures 7-9. Illustrations of heads of adult Gyrophaenina. Fig. 7. *Gyrophaena nana* Payk., A) dorsal aspect, B) ventral aspect (i.c.= infraorbital carina). Fig. 8. *Gyrophaena (Phaenogyra) gracilis* Seev., dorsal aspect. Fig. 9. *Gyrophaena sculptipennis* Csy., A) dorsal aspect, B) ventral aspect



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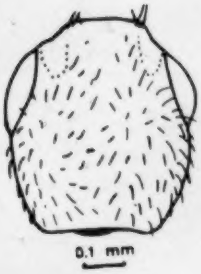

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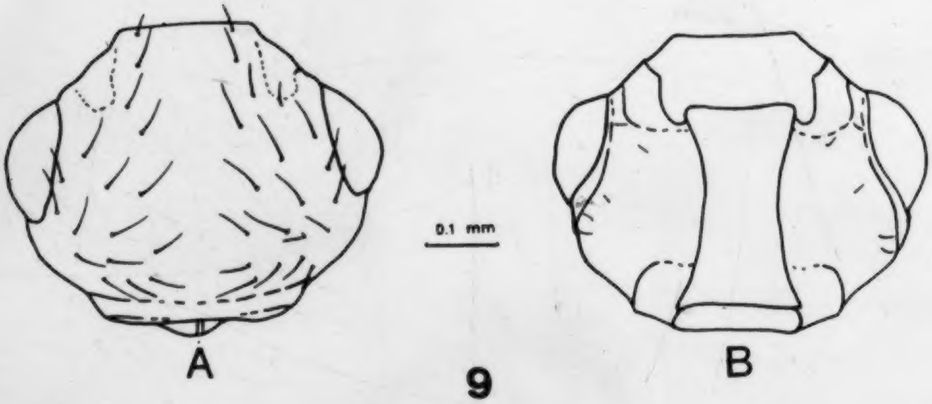

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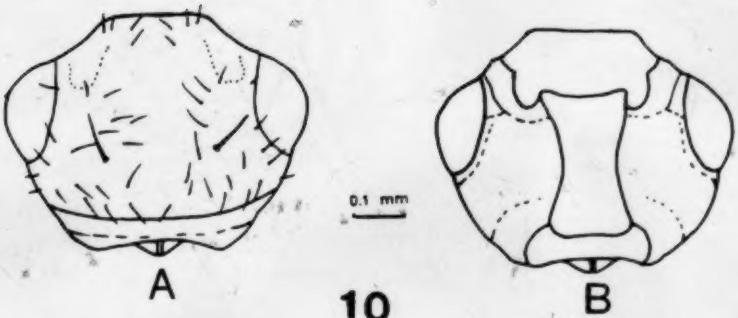
Figures 10-12. Illustrations of heads of adult Gyrophaenina. Fig. 10. *Gyrophaena egena* Csy., A) dorsal aspect, B) ventral aspect. Fig. 11. *Gyrophaena antennalis* Csy., A) dorsal aspect, B) ventral aspect. Fig. 12. *Phanerota fasciata* (Say), A) dorsal aspect, B) ventral aspect.



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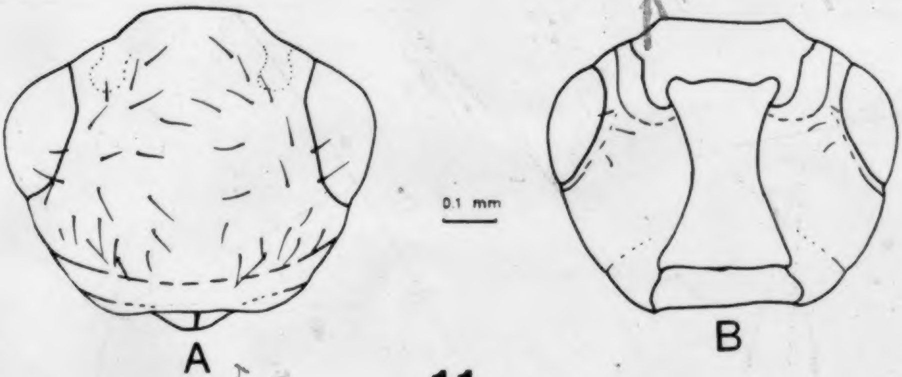

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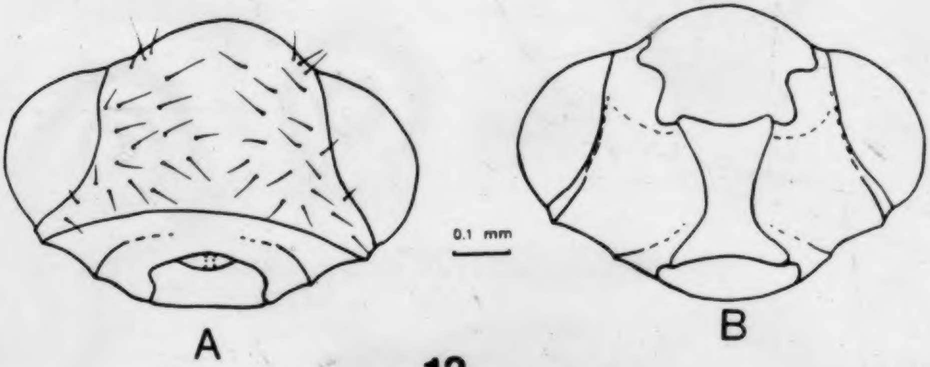

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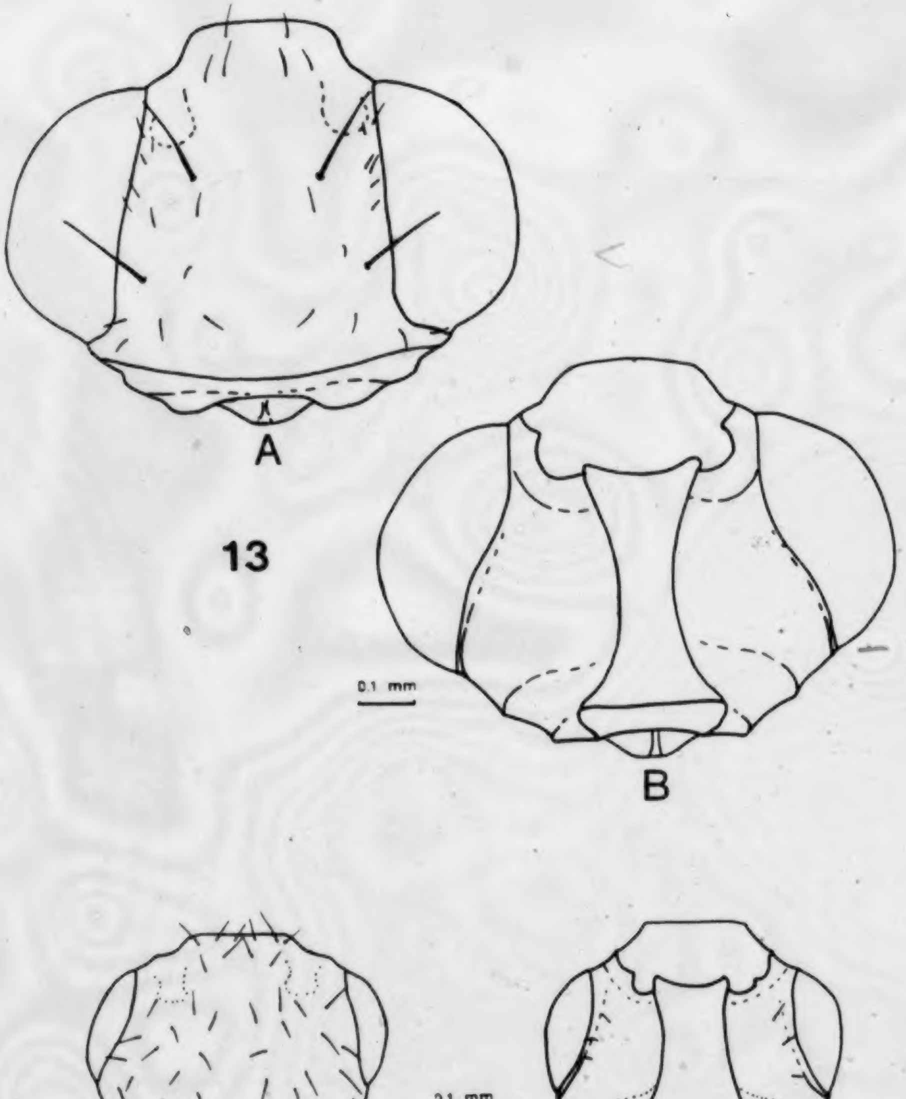
Figures 13-14. Illustrations of heads of adult Gyrophaenina. Fig. 13. *Phanerota (Acanthophaena) insigniventris* (Cam.), A) dorsal aspect, B) ventral aspect. Fig. 14. *Eumicrota corruscula* (Erichson), A) dorsal aspect, B) ventral aspect.



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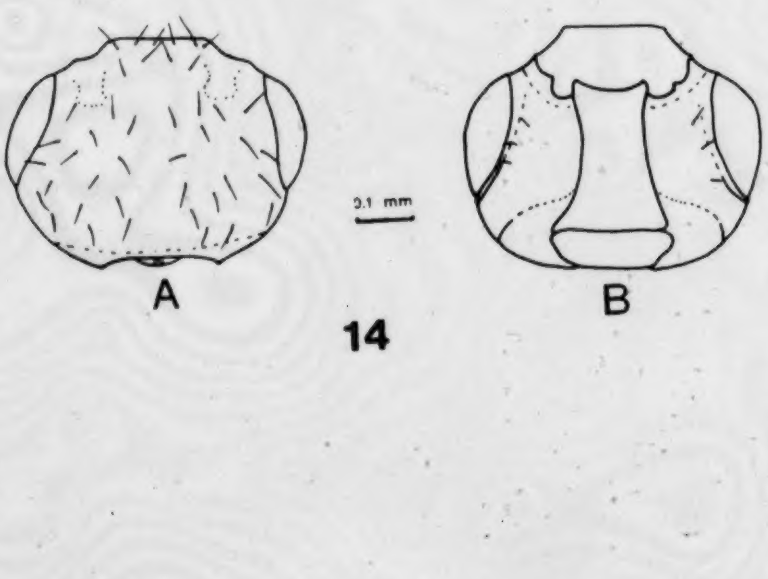

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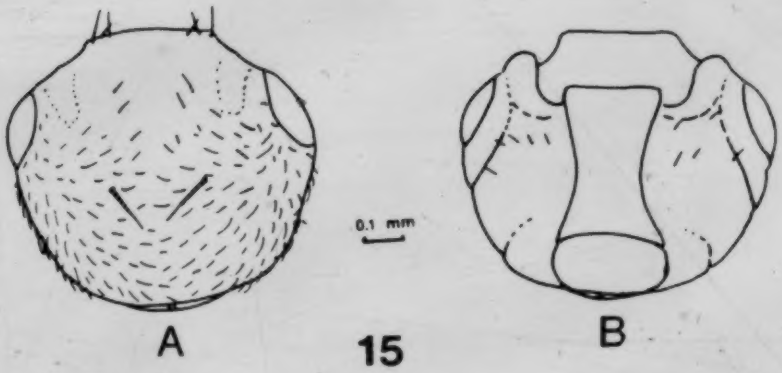
Figures 15-18. Illustrations of heads of adult Gyrophaenina. Fig. 15. *Brachida exigua* Heer., A) dorsal aspect, B) ventral aspect. Fig. 16. *Agaricochara laevicollis* Kr., A) dorsal aspect, B) ventral aspect. Fig. 17. *Sternotropa brevicornis* Cam., ventral aspect. Fig. 18. *Pseudoligota varians* Cam., ventral aspect.



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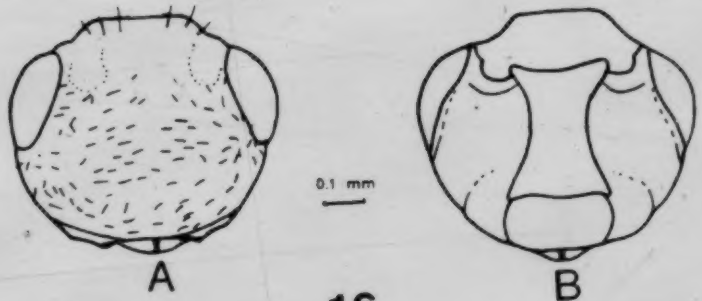

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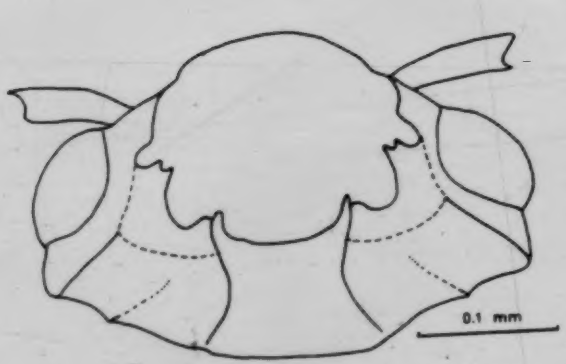

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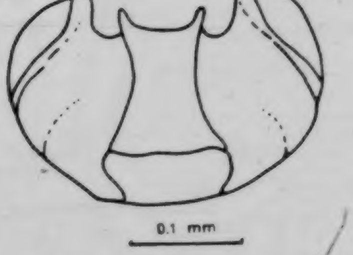

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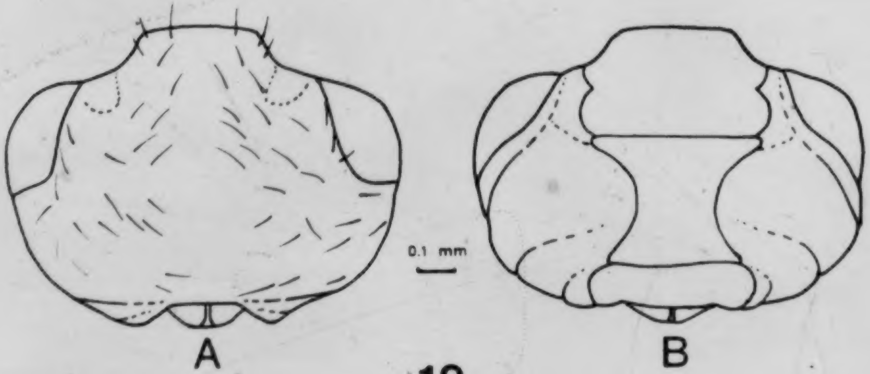
Figures 19-20. Illustrations of heads of adult Gyrophaenina. Fig. 19. *Brachycara* sp. (prob. *B. crassa* Sharp), A) dorsal aspect, B) ventral aspect. Fig. 20. *Agaricomorpha apachaena* (Seev.), A) dorsal aspect, B) ventral aspect.



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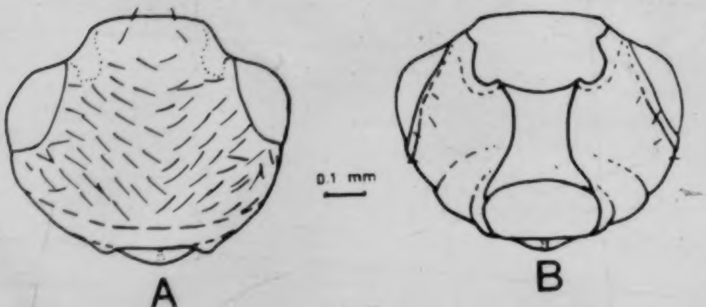

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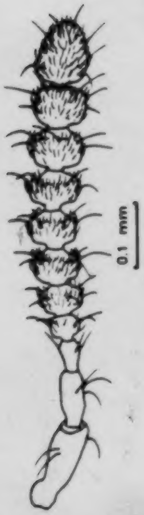
Figures 21-26. Illustrations of antennae of adult Gyrophaenina. Fig. 21. *Gyrophaena nana* Payk. Fig. 22. *Gyrophaena sculptipennis* Csy. Fig. 23. *Gyrophaena vitrina* Csy. Fig. 24. *Gyrophaena antennalis* Csy. Fig. 25. *Phanerota dissimilis* (Erichson). Fig. 26. *Eumicrota corruscula* (Erichson).



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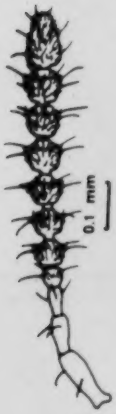

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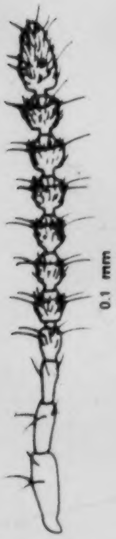

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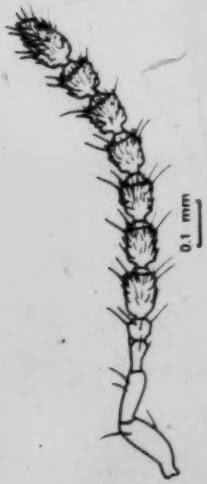

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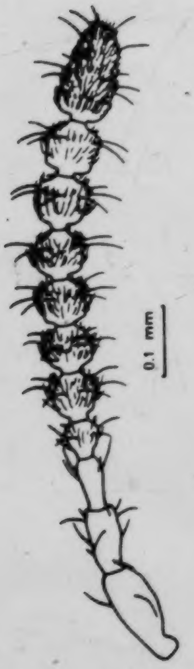

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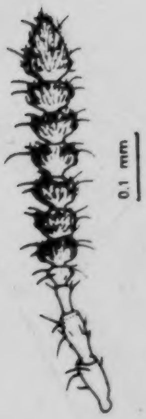

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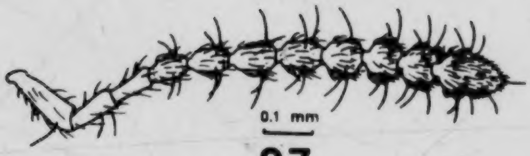
Figures 27-28. Illustrations of antennae of adult Gyrophaenina. Fig. 27. *Probrachida* undescr. sp. Fig. 28. *Agaricomorpha apachaena* (Seev.).

Figures 29-31. Illustrations of labra of adult Gyrophaenina. Fig. 29. *Gyrophaena affinis* Sahlb. Fig. 30. *Gyrophaena blackwelderi* Seev. Fig. 31. *Gyrophaena frosti* Seev.



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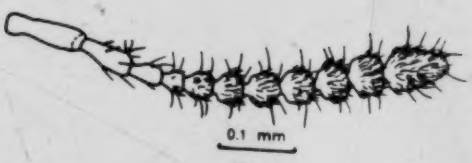

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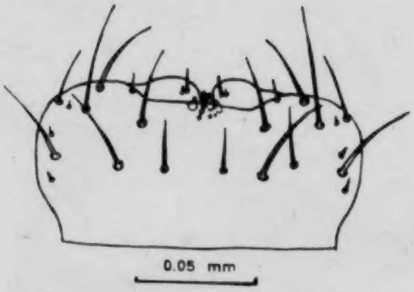

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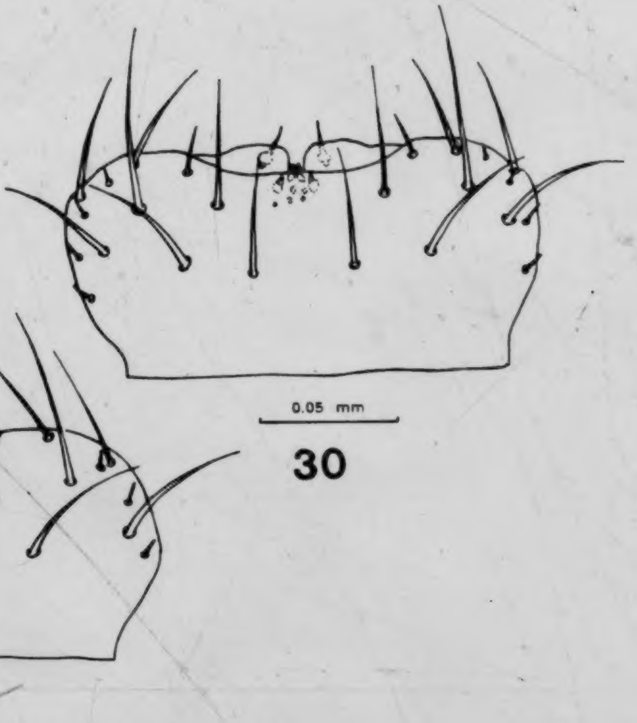

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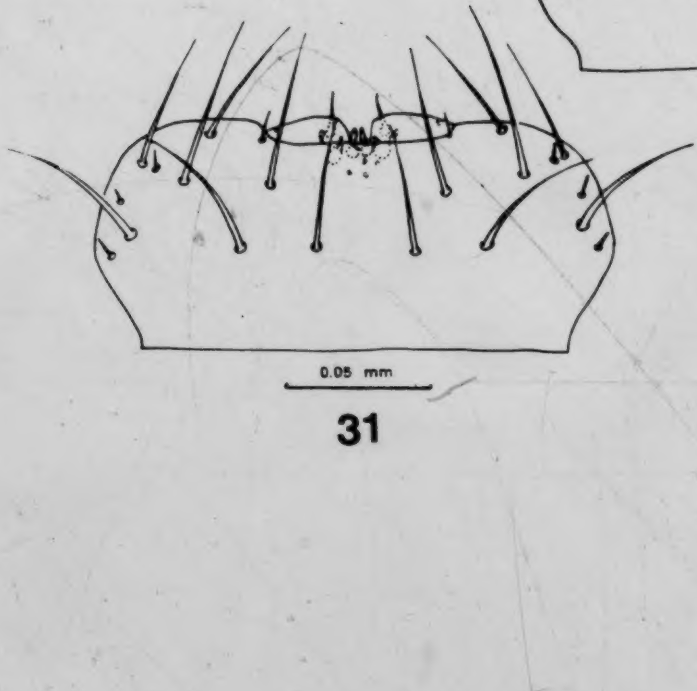

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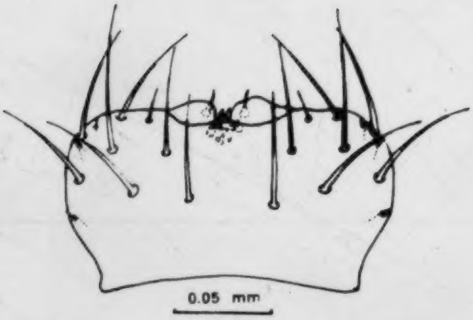
Figures 32-36. Illustrations of labra of adult Gyrophaenina. Fig. 32. *Gyrophaena antennalis* Csy. Fig. 33. *Phanerota fasciata* (Say). Fig. 34. *Phanerota dissimilis* (Erichson). Fig. 35. *Eumicrota corruscula* (Erichson). Fig. 36. *Encephalus americanus* Seev.



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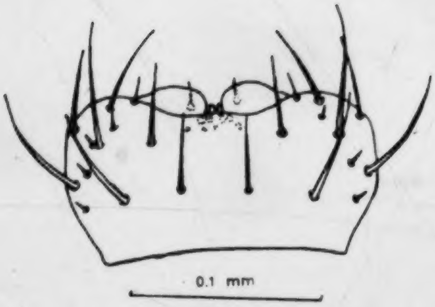

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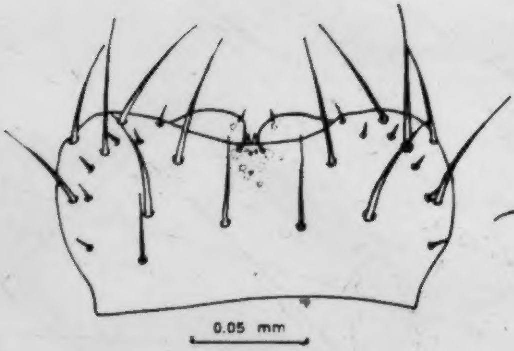

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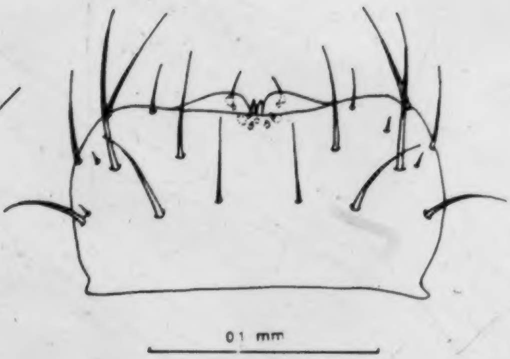

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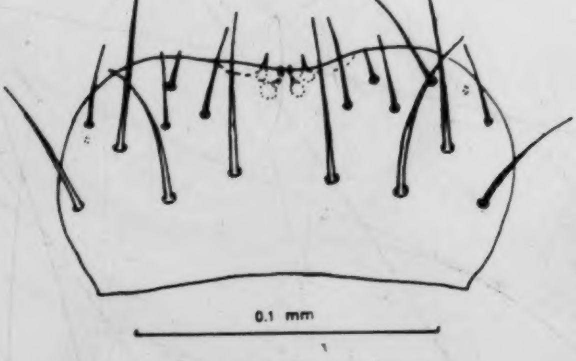

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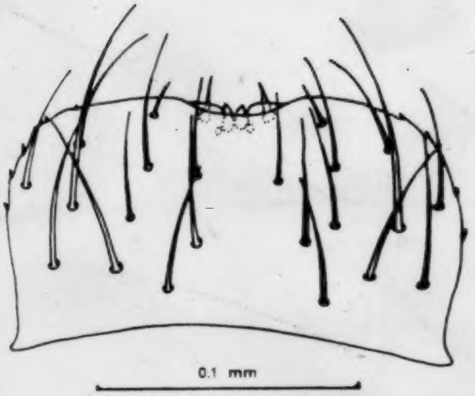
Figures 37-41. Illustrations of labra of adult Gyrophaenina. Fig. 37. *Probrachida modesta* (Sharp). Fig. 38. *Probrachida carinata* (Sharp). Fig. 39. *Probrachida sparsa* (Sharp). Fig. 40. *Probrachida geniculata* (Sharp). Fig. 41. *Probrachida* undescr. sp.



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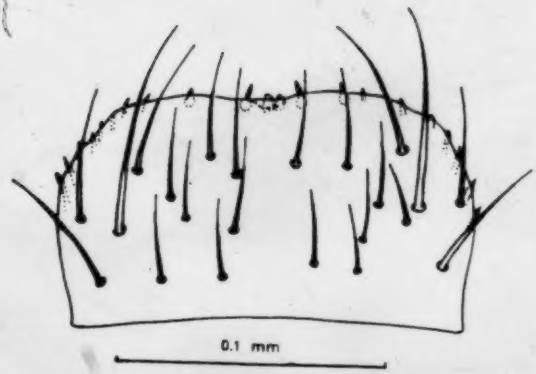

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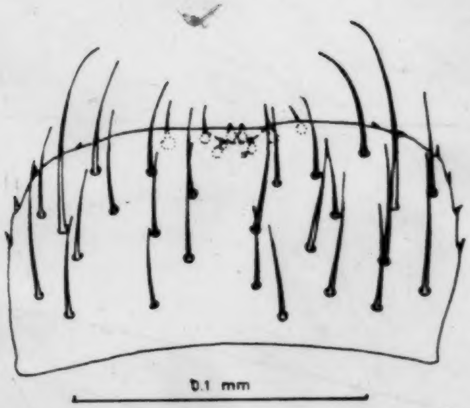

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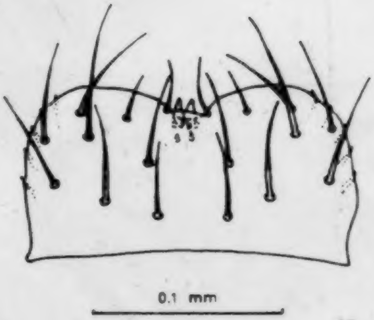

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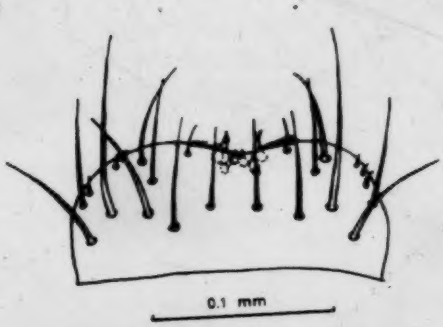

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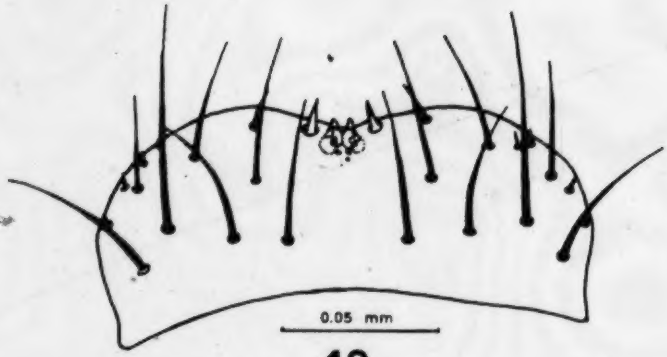
Figures 42-46. Illustrations of labra of adult Gyrophaenina. Fig. 42. *Brachida exigua* Heer. Fig. 43. *Brachida densiventris* Bernh. Fig. 44. *Brachida natalensis* Bernh. Fig. 45. *Brachida sublaevipennis* Cam. Fig. 46. *Brachida africana* Bernh.



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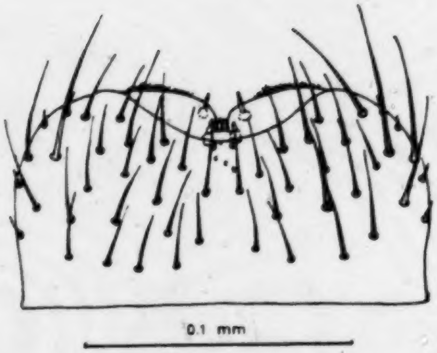

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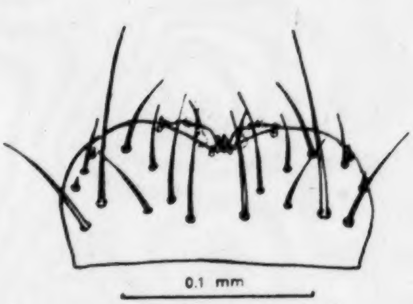

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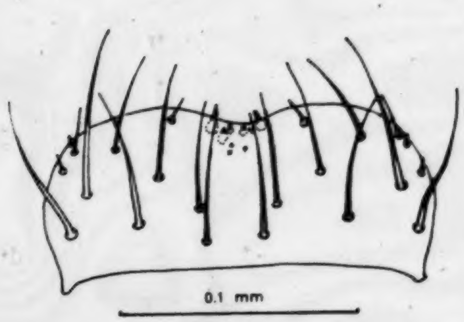

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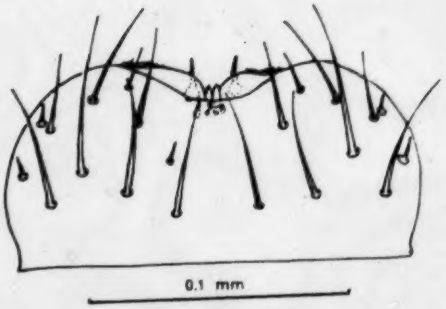

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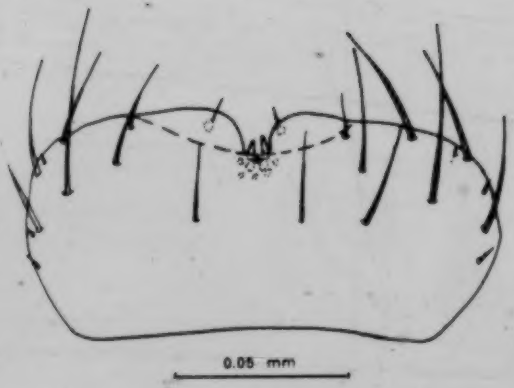
Figures 47-52. Illustrations of labra of adult Gyrophaenina. Fig. 47. *Agaricochara laevicollis* Kr. Fig. 48. *Sternotropa brevicornis* Cam. Fig. 49. *Sternotropa flavicornis* Cam. Fig. 50. *Sternotropa apicalis* Cam. Fig. 51. *Pseudoligota varians* Cam. Fig. 52. *Pseudoligota affinis* Cam.



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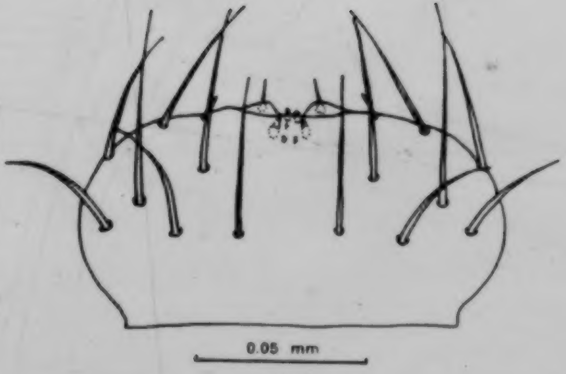

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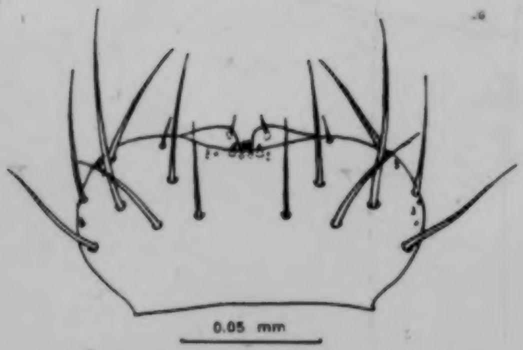

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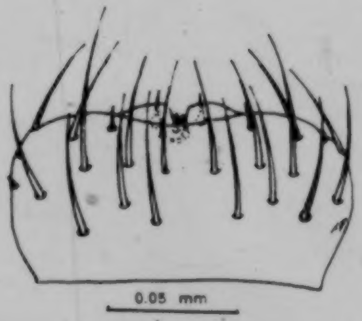

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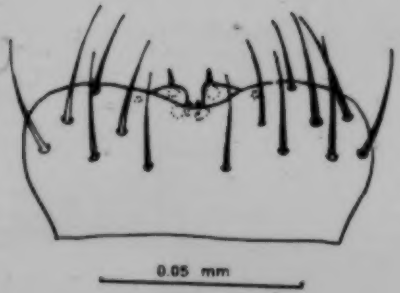

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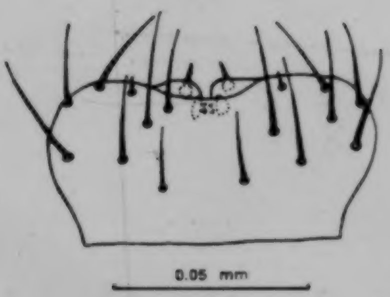

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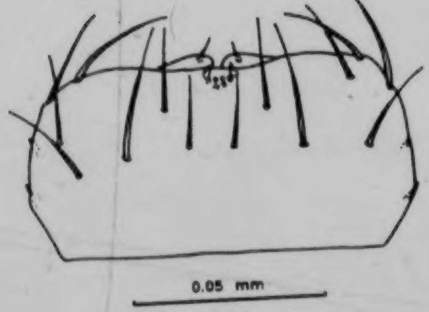
Figures 53-55. Illustrations of labra of adult Gyrophaenina. Fig. 53. *Adelarthra barbari* Cam. Fig. 54. *Brachycara* sp. (prob. *B. crassa* Sharp). Fig. 55. *Agaricomorpha apachaena* (Seev.).

Figures 56-57. Illustrations of mandibles of adult Gyrophaenina. Fig. 56. *Gyrophaena vitrina* Csy., right (b.s.= bifid structures, i.t.= internal tooth, m.a.= molar area). Fig. 57. *Phanerota fasciata* (Say), right.



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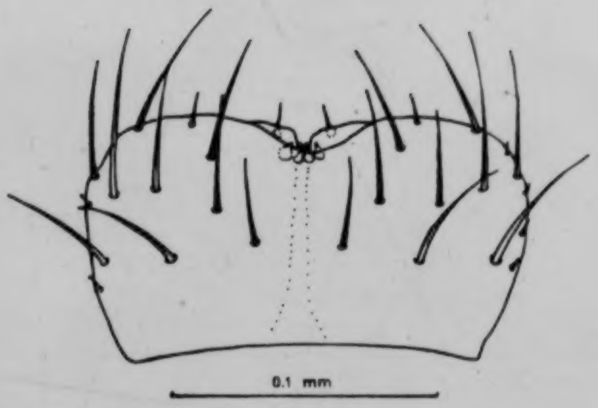

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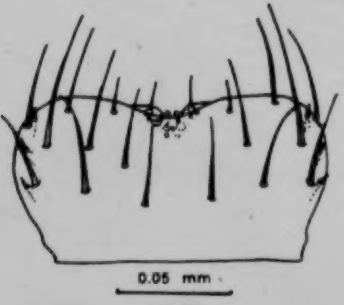

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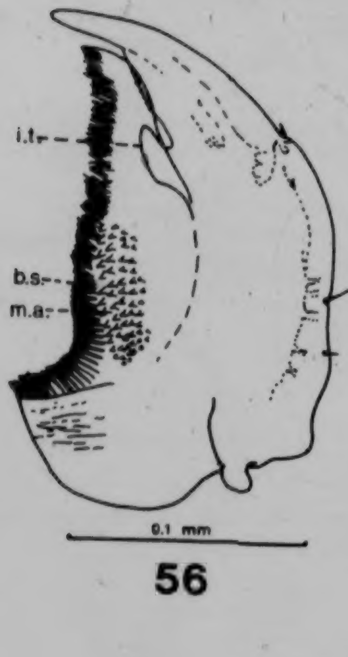
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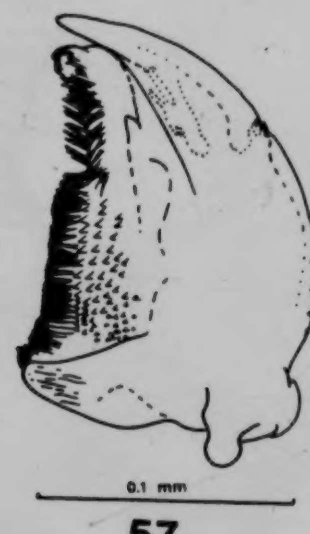

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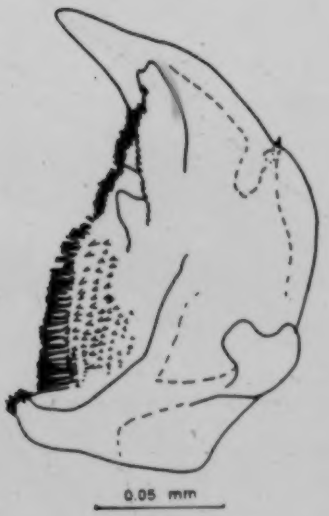
Figures 58-61. Illustrations of mandibles of adult Gyrophaenina. Fig. 58. *Phanerota (Acanthophaena) insigniventris* (Cam.), right. Fig. 59. *Eumicrota corruscula* (Erichson), right. Fig. 60. *Encephalus complicans* Kirby, right. Fig. 61. *Encephalus zealandicus* Broun, right.



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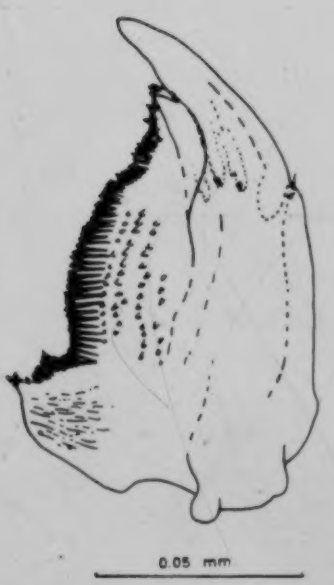

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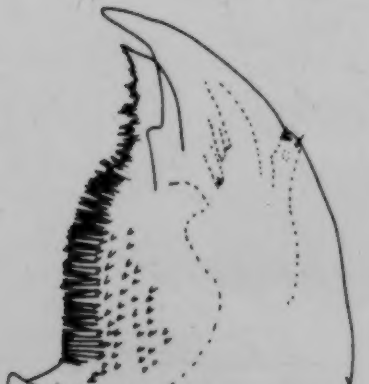

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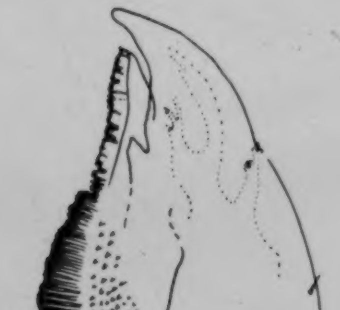

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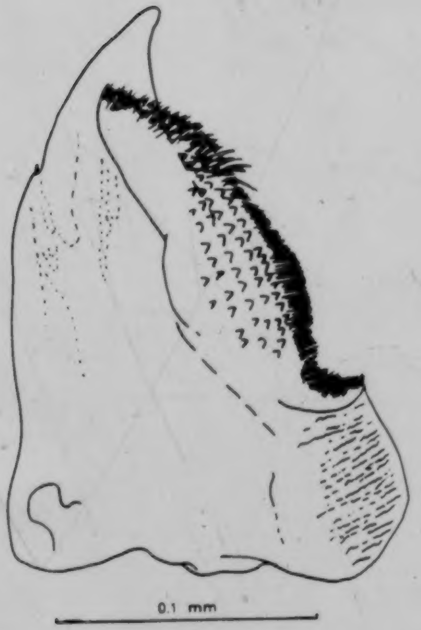
Figures 62-65. Illustrations of mandibles of adult Gyrophaenina. Fig. 62. *Probrachida modesta* (Sharp), left. Fig. 63. *Probrachida geniculata* (Sharp), left. Fig. 64. *Probrachida* undescr. sp., left. Fig. 65. *Brachida exigua* Heer., left.



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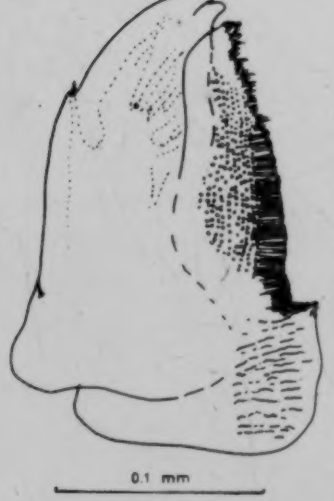

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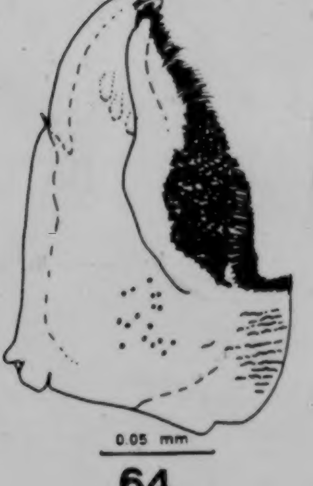

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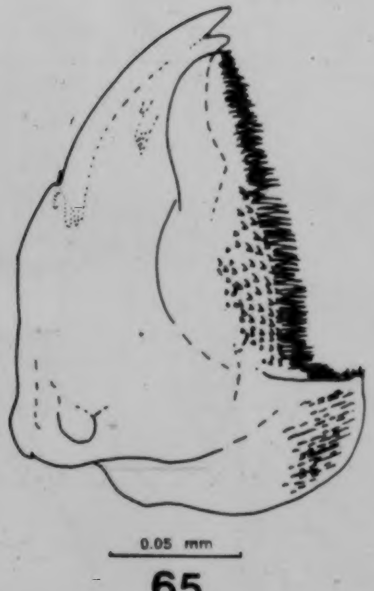

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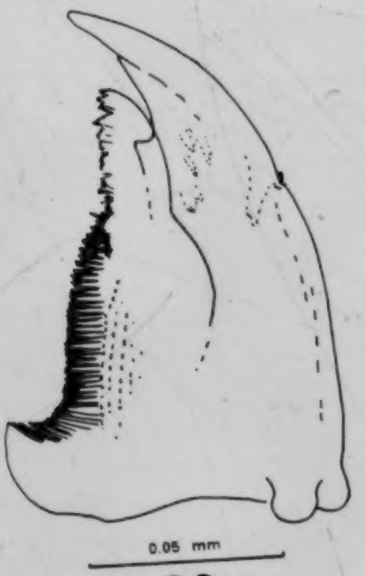
Figures 66-69. Illustrations of mandibles of adult Gyrophaenina. Fig. 66. *Agaricochara laevicollis* Kr., right. Fig. 67. *Sternotropa brevicornis* Cam., left. Fig. 68. *Sternotropa flavicornis* Cam., right. Fig. 69. *Sternotropa apicalis* Cam., right.



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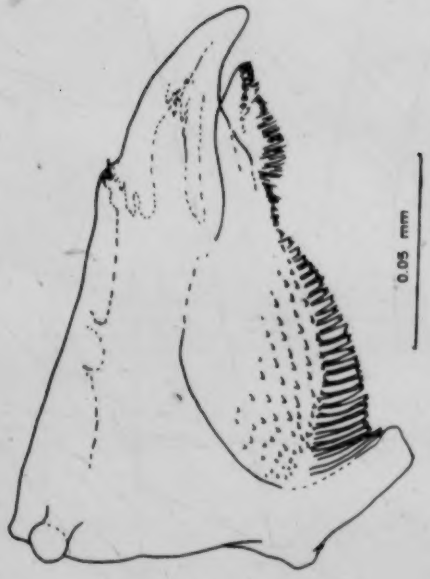

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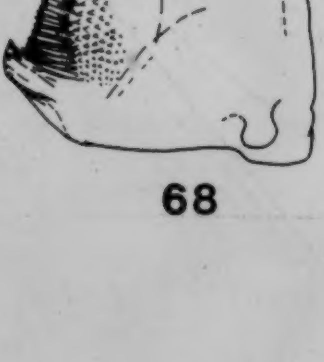

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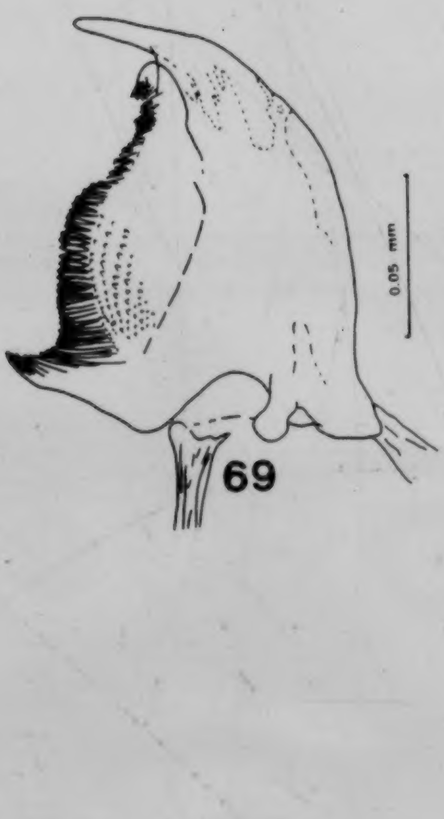

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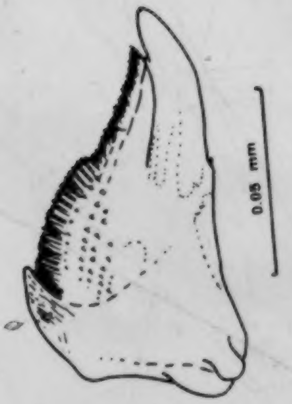
Figures 70-72. Illustrations of mandibles of adult Gyrophaenina. Fig. 70. *Pseudoligota affinis* Cam., right. Fig. 71. *Brachycara* sp. (prob. *B. crassa* Sharp), right. Fig. 72. *Agaricomorpha apachaena* (Seev.), right.



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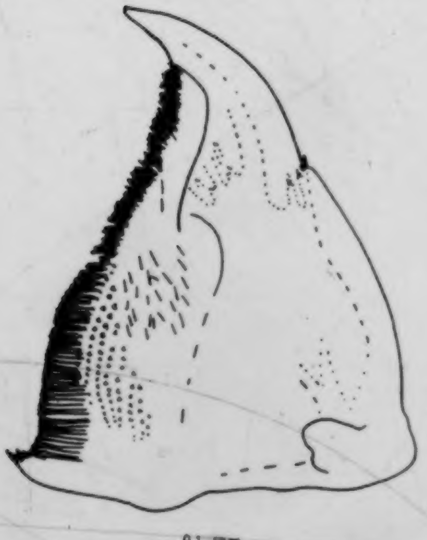

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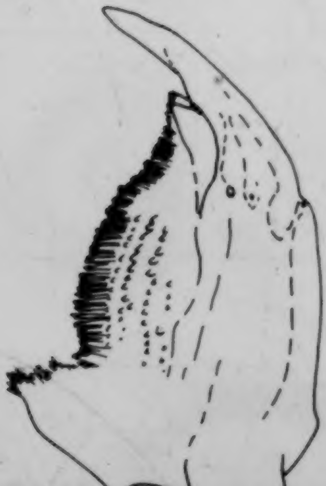

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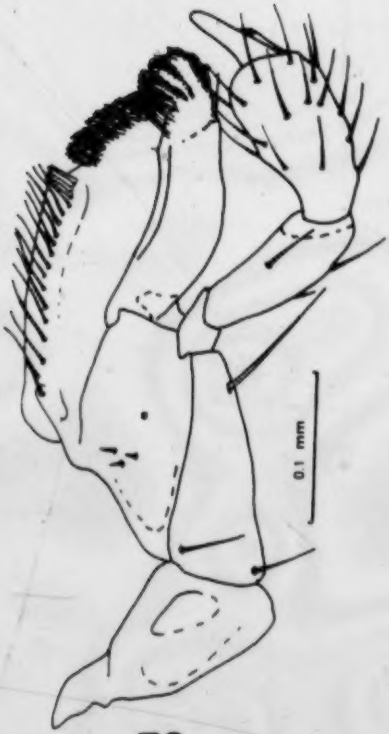
Figures 73-75. Illustrations of maxillae of adult Gyrophaenina. Fig. 73. *Gyrophaena antennalis* Csy. Fig. 74. *Gyrophaena affinis* Sahlb. Fig. 75. *Phanerota fasciata* (Say).



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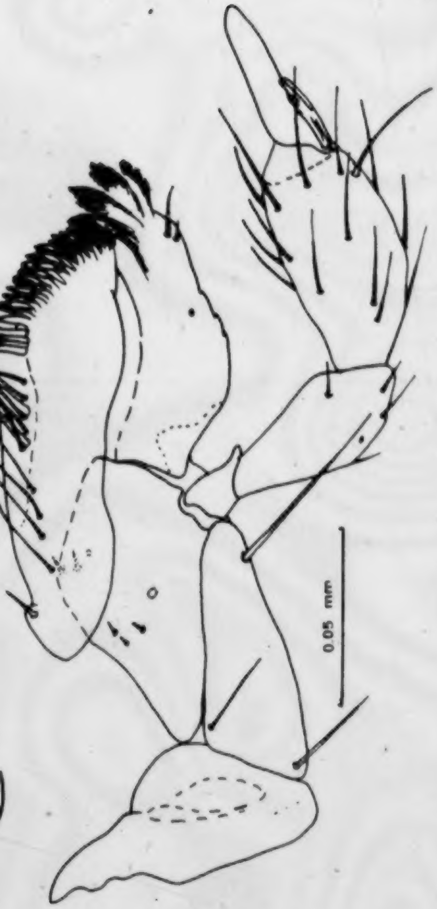

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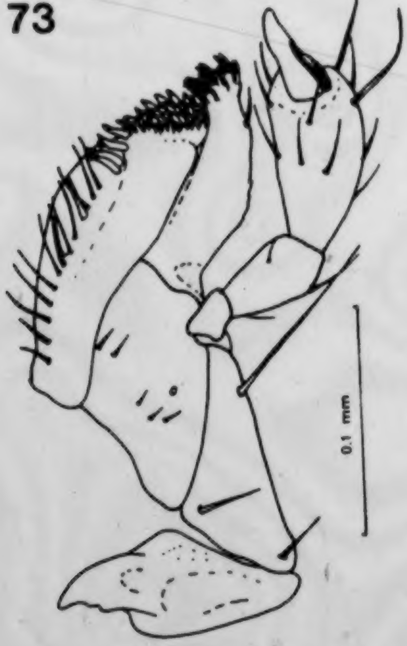

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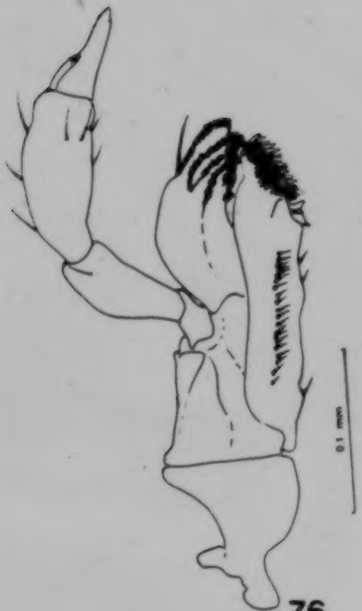

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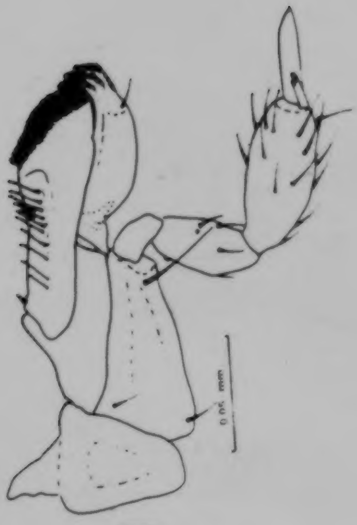

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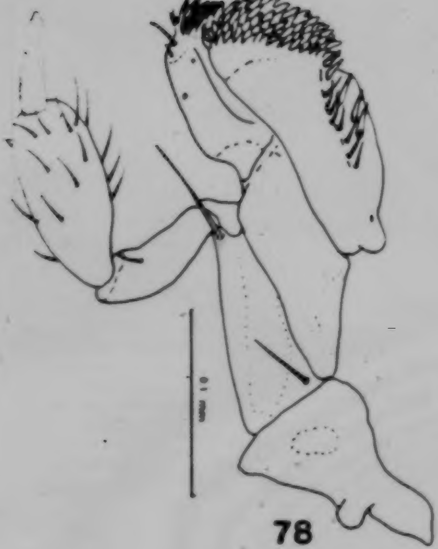

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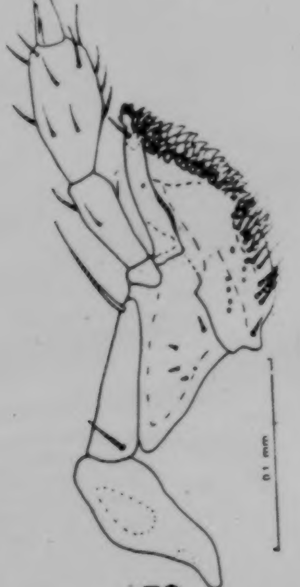

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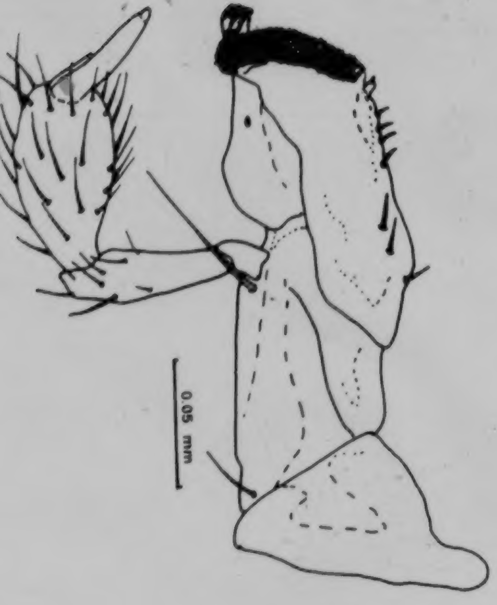

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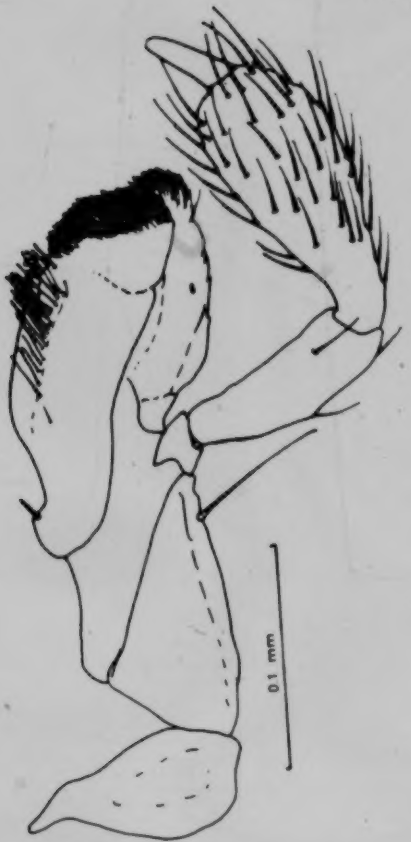

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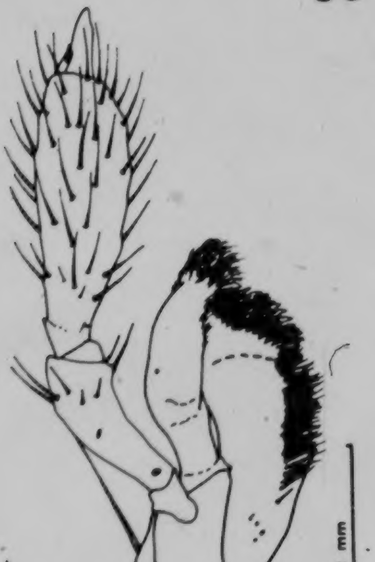

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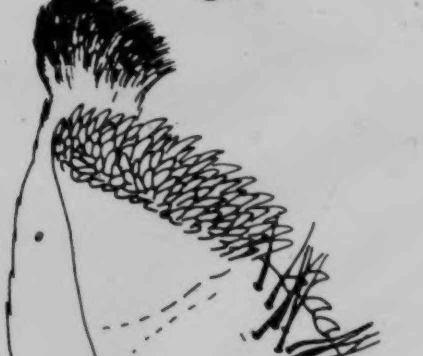

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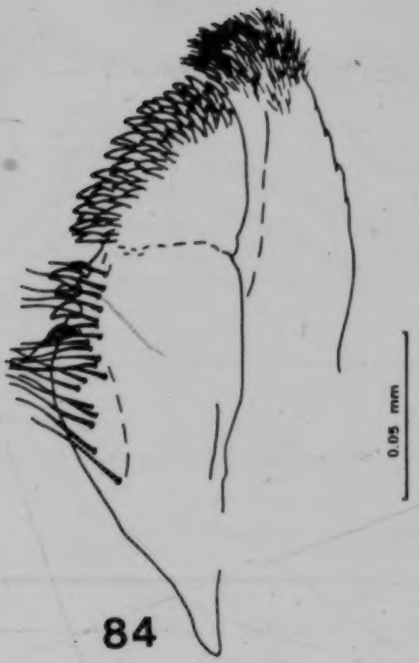
Figures 84-87. Illustrations of maxillae of adult Gyrophaenina. Fig. 84. *Probrachida carinata* (Sharp), detail of galea and lacinia. Fig. 85. *Brachida exigua* Heer., detail of lacinia. Fig. 86. *Brachida densiventris* Bernh. Fig. 87. *Brachida natalensis* Bernh.



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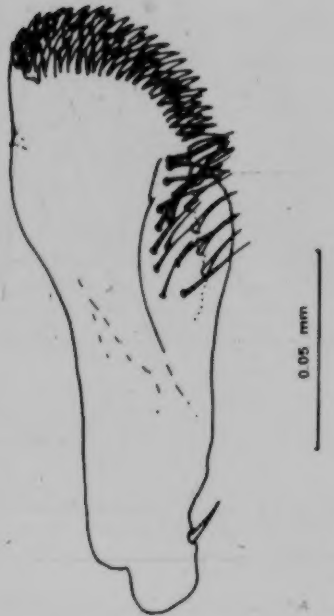

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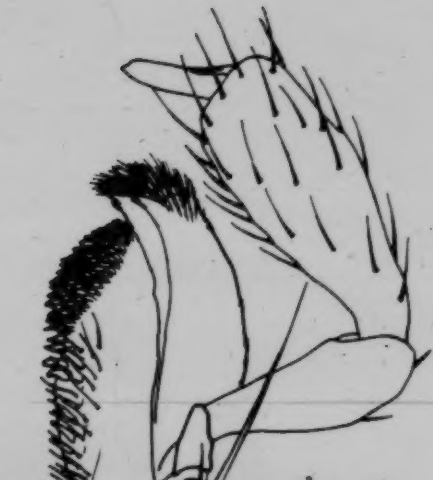

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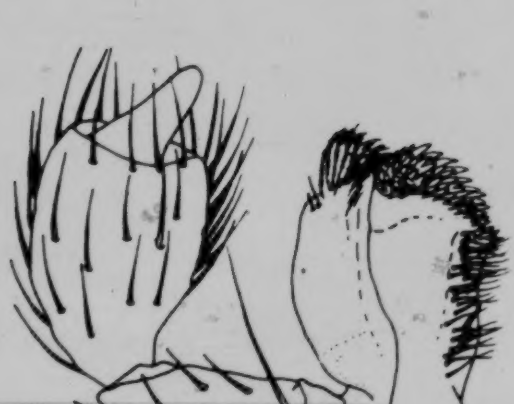

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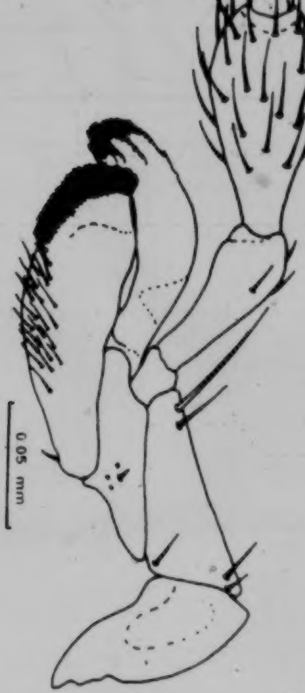

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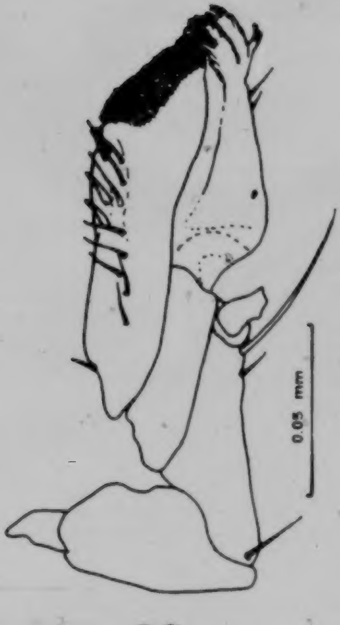

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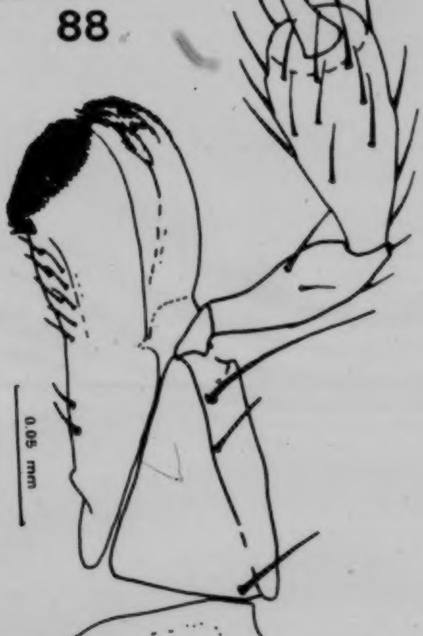

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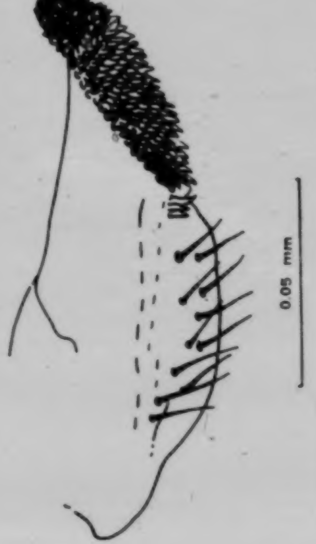

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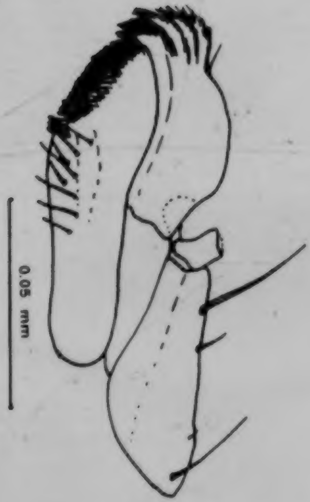

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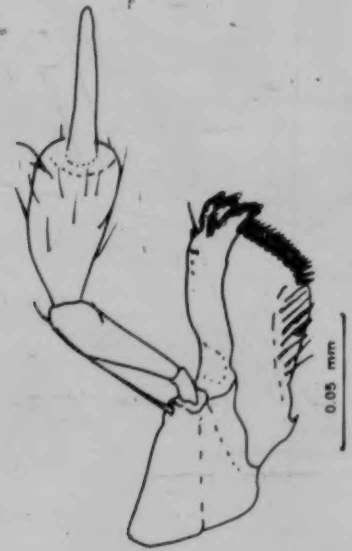

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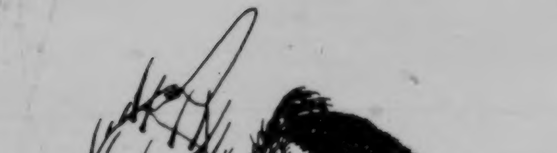

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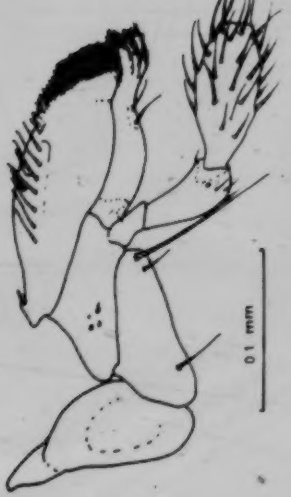

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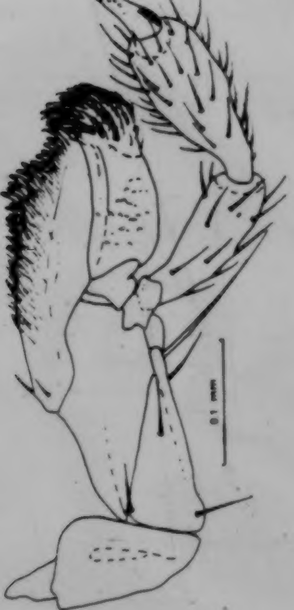
Figures 96-97. Illustrations of maxillae of adult Bolitocharina. Fig. 96. *Bolitochara lunulata* Gyll. Fig. 97. *Venusa* sp.

Figures 98-99. Illustrations of labia of adult Gyrophaenina. Fig. 98. *Gyrophaena antennalis* Csy. Fig. 99. *Gyrophaena vitrina* Csy.



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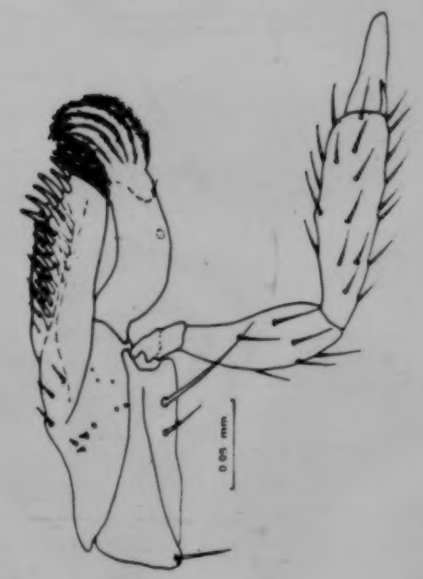

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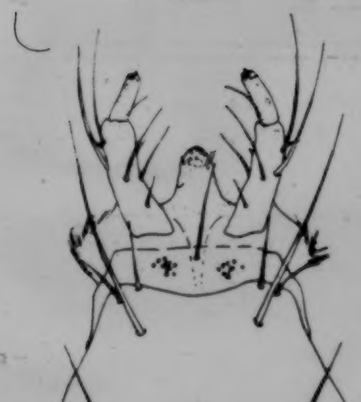

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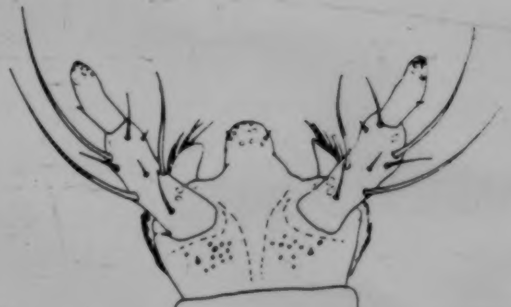

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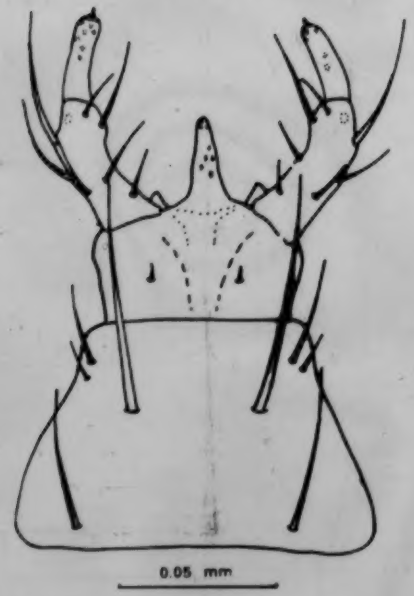
Figures 100-104. Illustrations of labia of adult Gyrophaenina. Fig. 100. *Phanerota fasciata* (Say). Fig. 101. *Phanerota (Acanthophaena) insigniventris* (Cam.) Fig. 102. *Eumicrota corruscula* (Erichson). Fig. 103. *Encephalus complicans* Kirby. Fig. 104. *Encephalus zealandicus* Broun.



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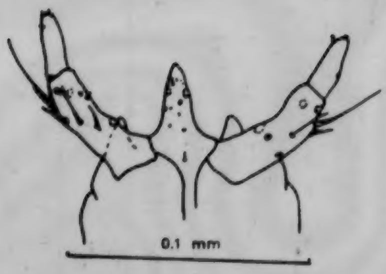

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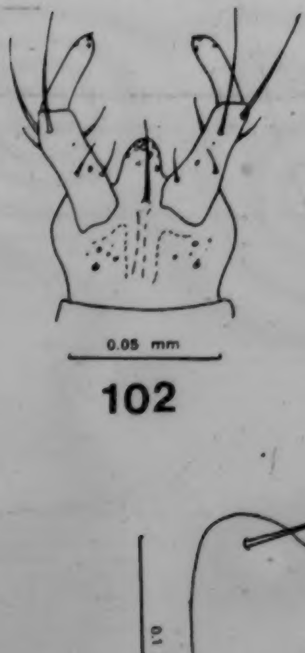

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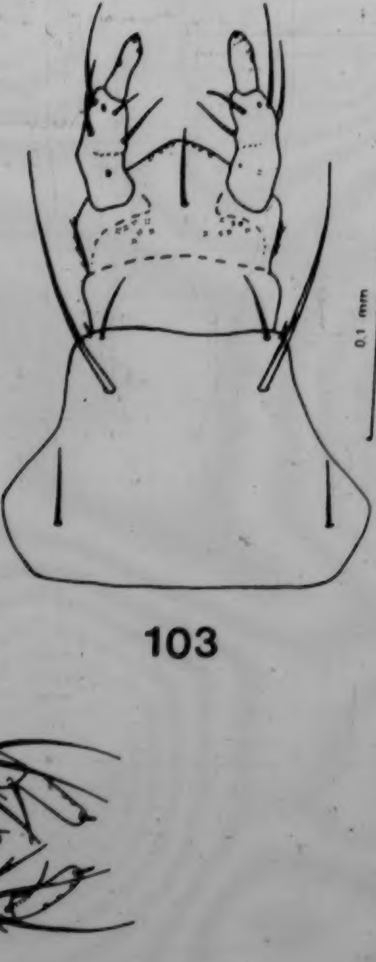

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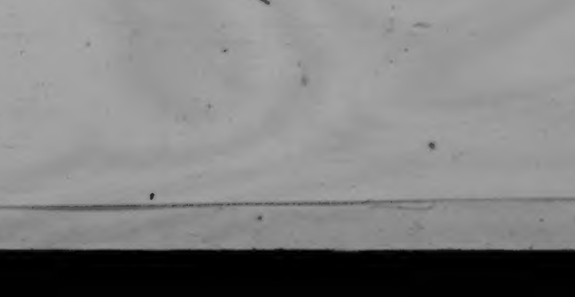

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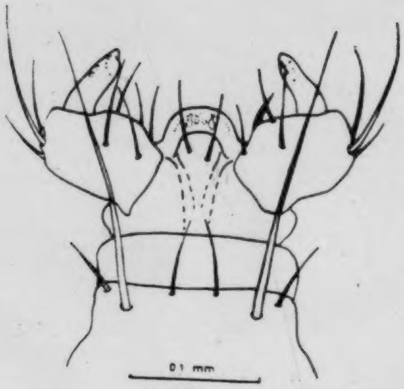
Figures 105-109 Illustrations of labia of adult Gyrophaenina. Fig. 105. *Probrachida modesta* (Sharp). Fig. 106. *Probrachida carinata* (Sharp). Fig. 107. *Probrachida* undescr. sp. Fig. 108. *Brachida exigua* Heer. Fig. 109. *Brachida africana* Bernh.



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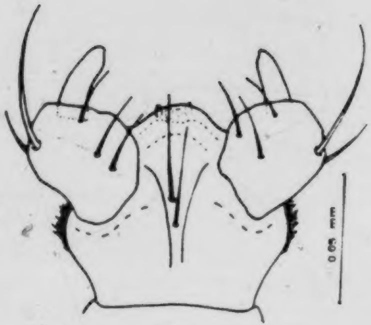

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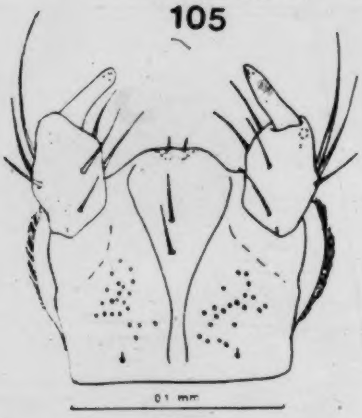

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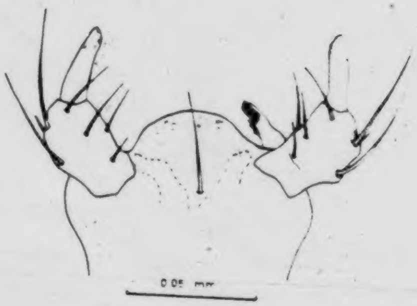

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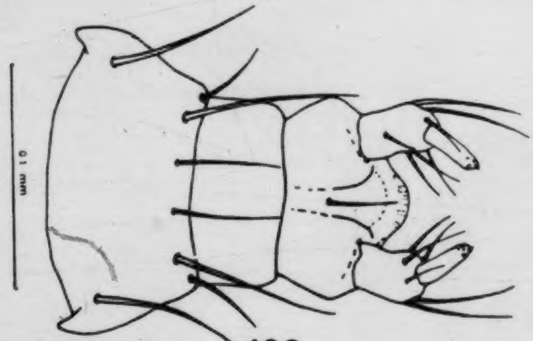

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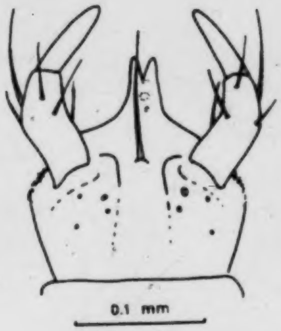
Figures 110-115 Illustrations of labia of adult Gyrophaenina. Fig. 110. *Agaricochara laevicollis* Kr. Fig. 111. *Sternotropa brevicornis* Cam. Fig. 112. *Sternotropa apicalis* Cam. Fig. 113. *Pseudoligota varians* Cam. Fig. 114. *Adelarthra barbari* Cam. Fig. 115. *Neobrachida castanea* Cam.



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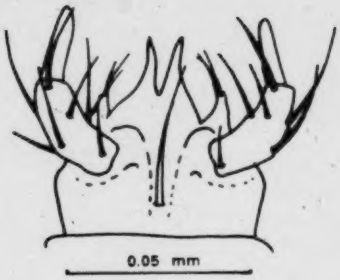

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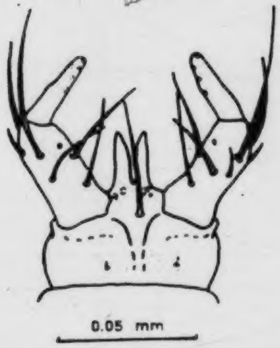

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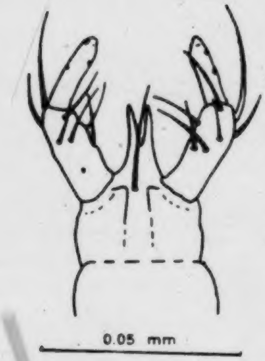

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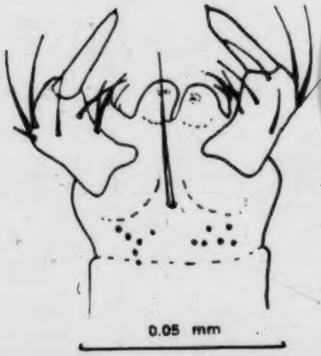

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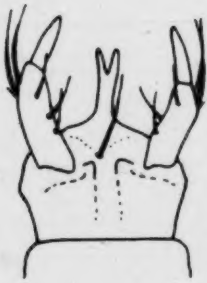

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Figures 116-118. Illustrations of labia of adult Gyrophaenina. Fig. 116. *Brachycara* sp. (prob. *B. crassa* Sharp). Fig. 117. *Agaricomorpha apachaena* (Seev.). Fig. 118. *Bolitochara lunulata* Gyll.

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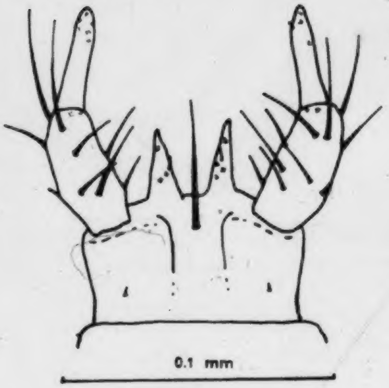

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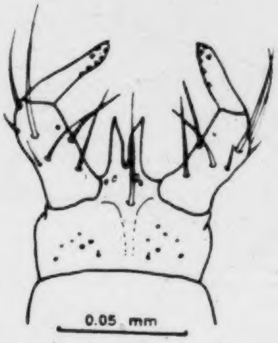

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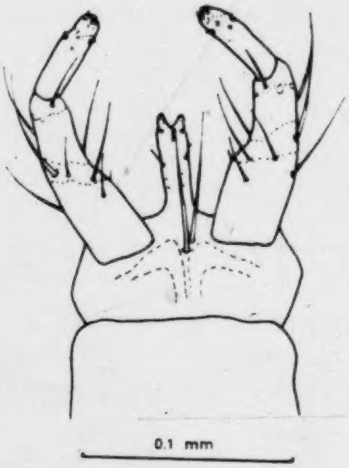

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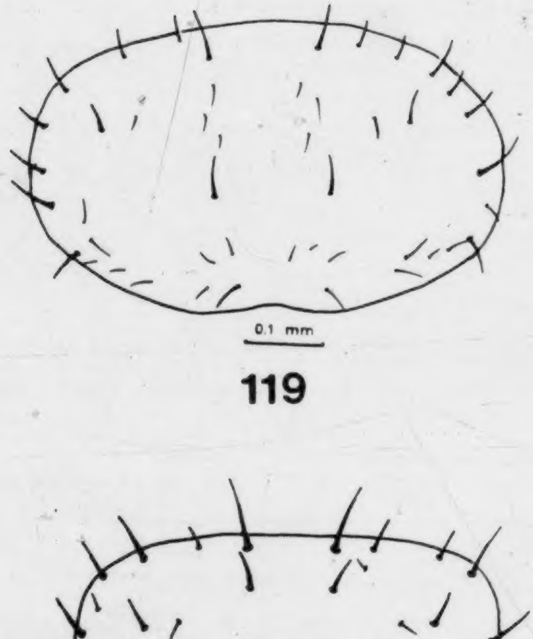

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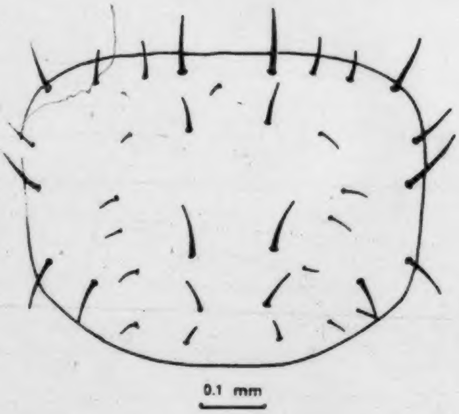

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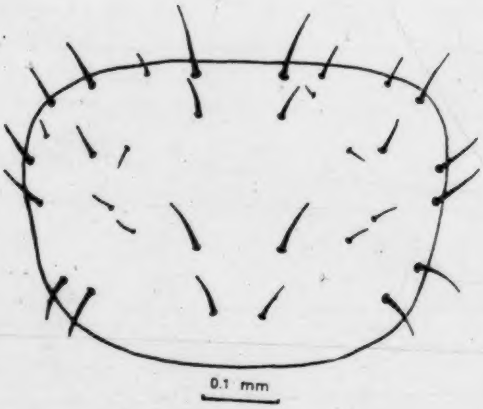

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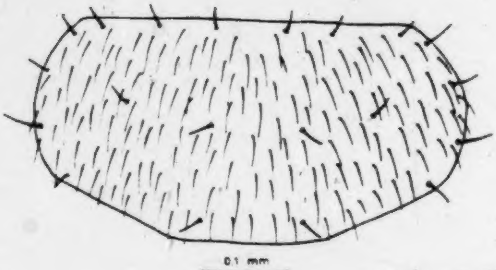

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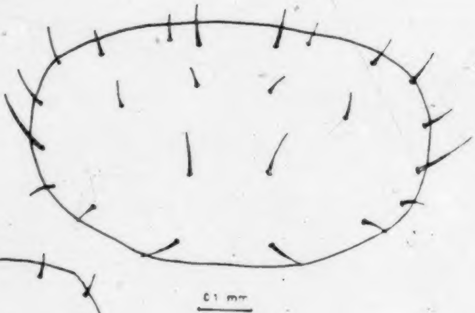

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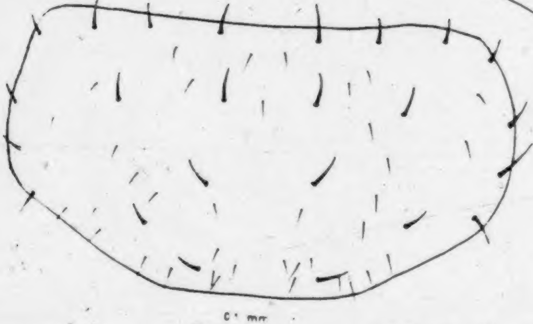

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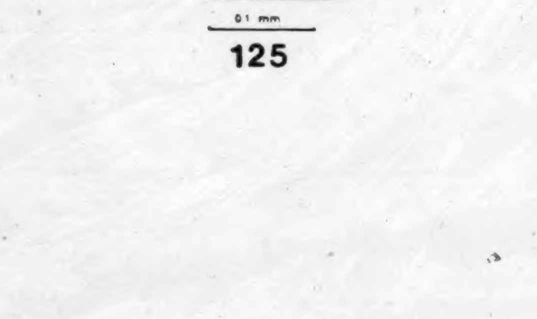

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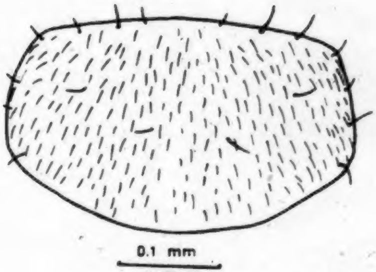
Figures 126-130. Illustrations of of dorsal aspect of pronota of adult Gyrophaenina. Fig. 126. *Agaricochara laevicollis* Kr. Fig. 127. *Sternotropa brevicornis* Cam. Fig. 128. *Pseudoligota varians* Cam. Fig. 129. *Brachycara* sp. (prob. *B. crassa* Sharp). Fig. 130. *Agaricomorpha apachaena* (Seev.).



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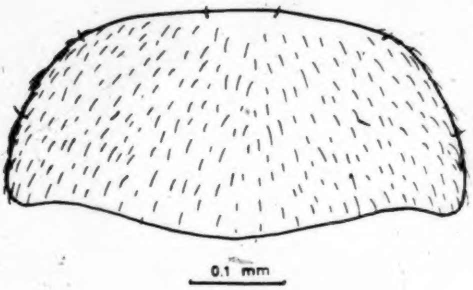

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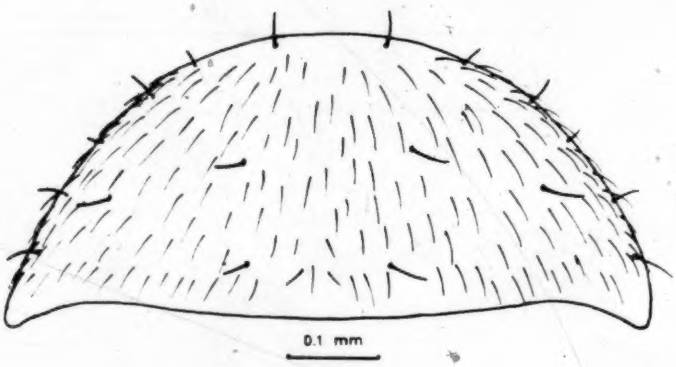

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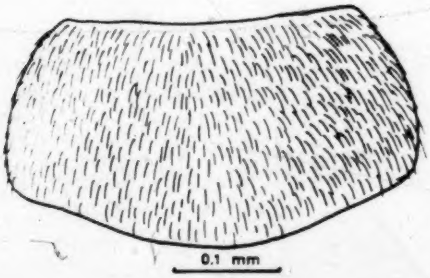

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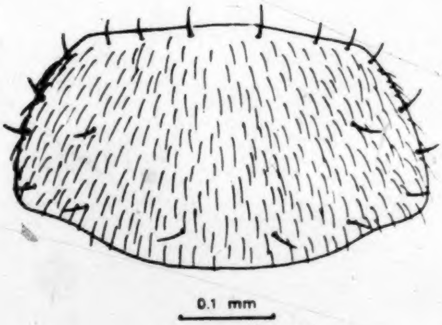

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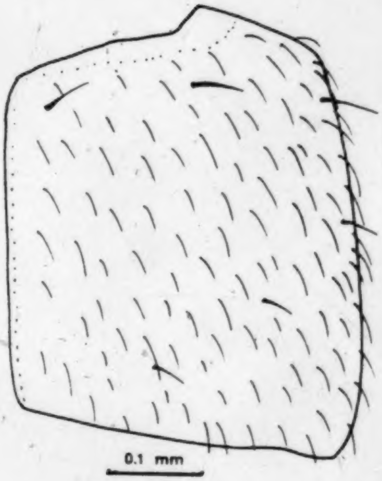

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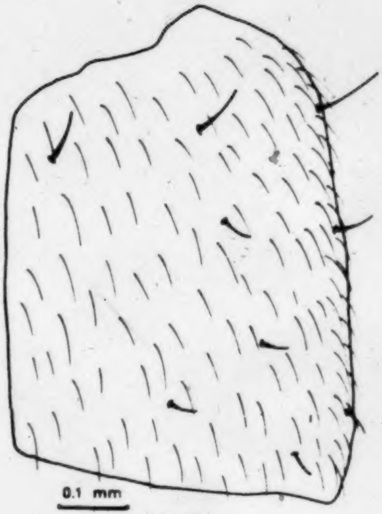

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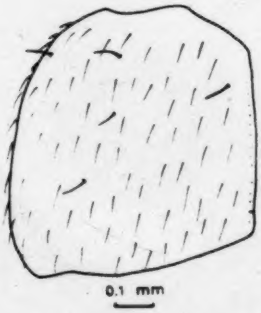

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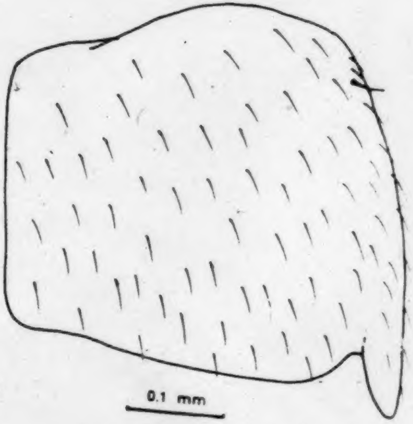

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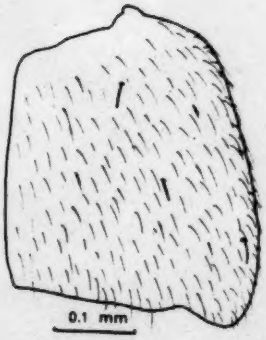

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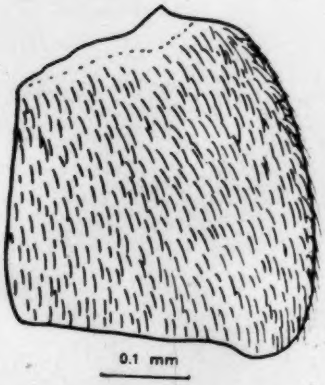

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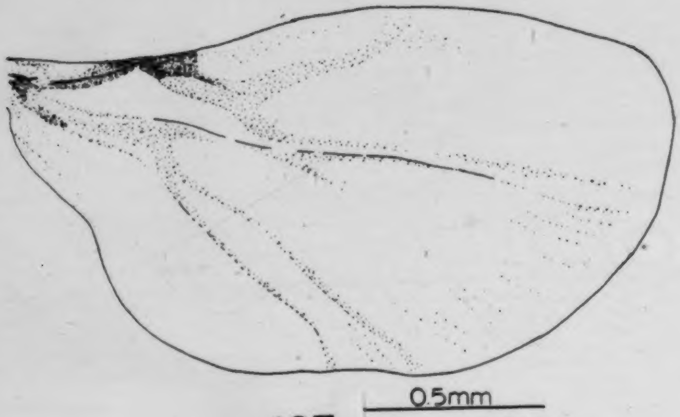

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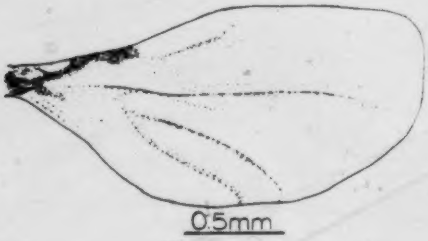

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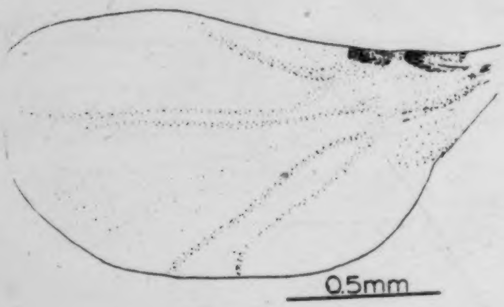

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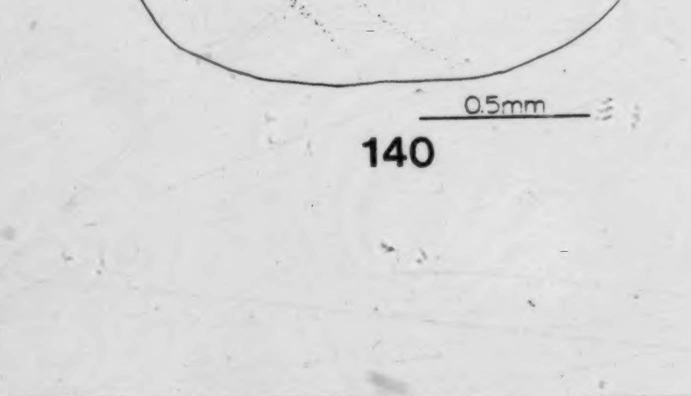

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Figure 141. Illustration of wing of members of *Venusa* sp. (subtribe Bolitocharina).

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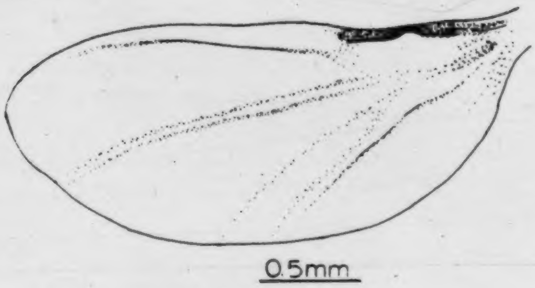

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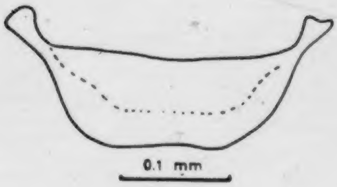

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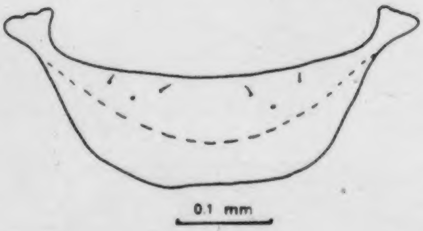

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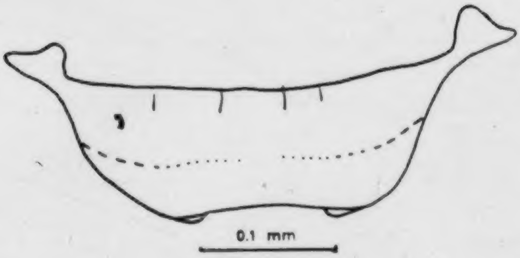

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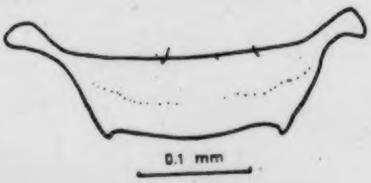

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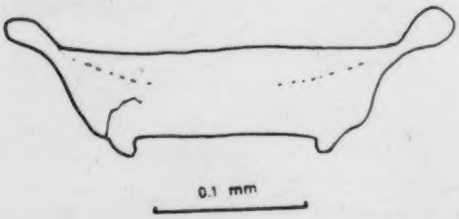

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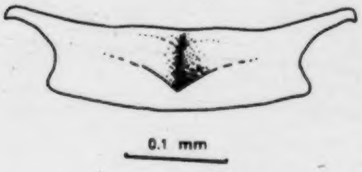
Figures 149-152. Illustrations of meso- and metasterna of adult Gyrophaenina. Fig. 149. *Gyrophaena nana* Payk. Fig. 150. *Gyrophaena blackwelderi* Seev. Fig. 151. *Phanerota fasciata* (Say). Fig. 152. *Agaricochara laevicollis* Kr.



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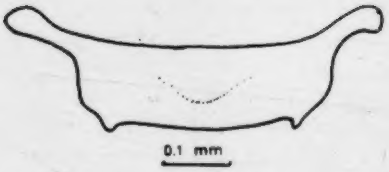

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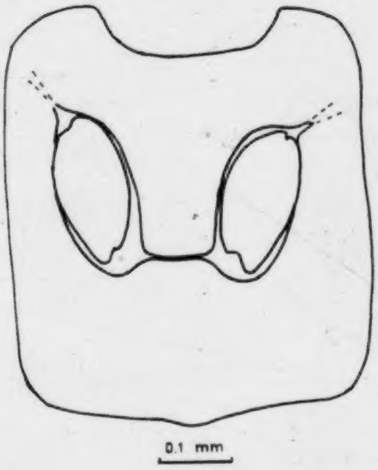

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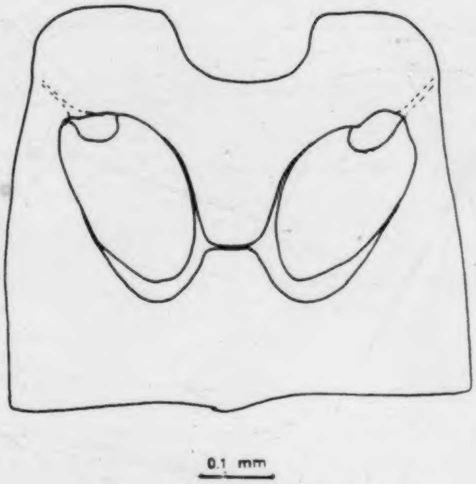

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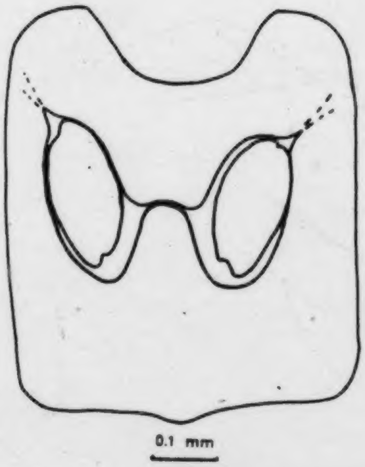

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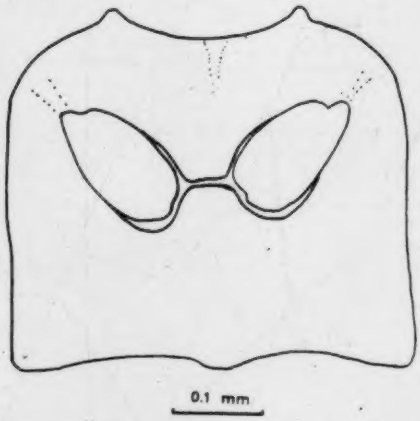

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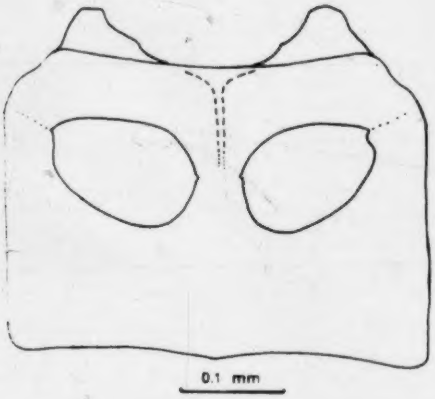
Figures 153-155. Illustrations of meso- and metasterna of adult Gyrophaenina. Fig. 153. *Sternotropa brevicornis* Cam. Fig. 154. *Pseudoligota varians* Cam. Fig. 155. *Agaricomorpha apachaena* (Seev.).



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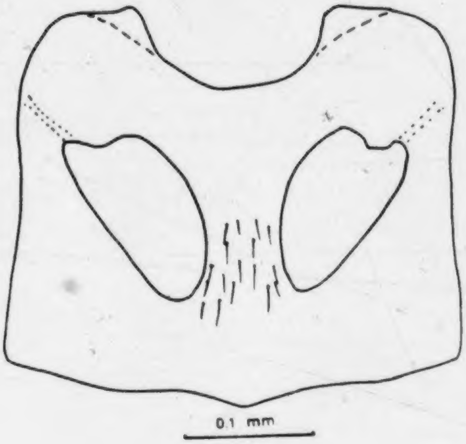

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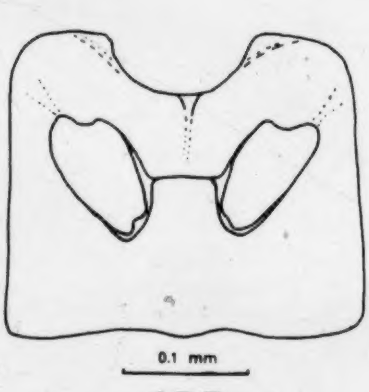

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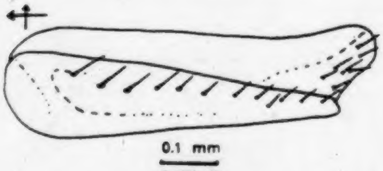
Figure 161. *Phanerota dissimilis* (Erichson), hind tarsus.



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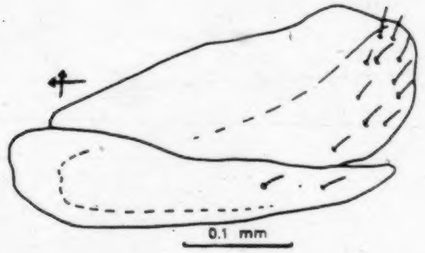

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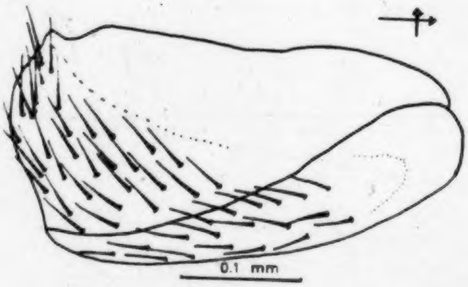

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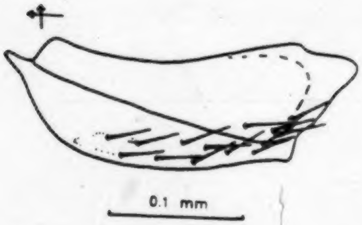

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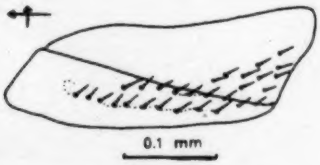

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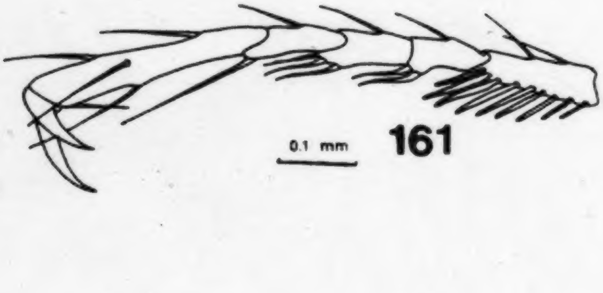

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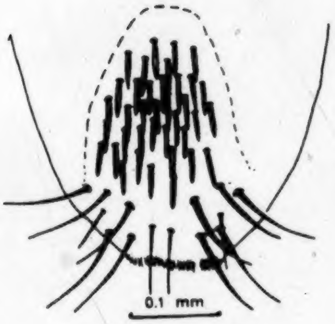
Figures 162-167 Illustrations of tergum 10 of adult Gyrophaenina. Fig. 162. *Gyrophaena antennalis* Csy. Fig. 163. *Gyrophaena blackwelderi* Seev. Fig. 164. *Phanerota fasciata* (Say). Fig. 161. *Phanerota dissimilis* (Erichson). Fig. 166. *Eumicrota corruscula* (Erichson). Fig. 167. *Encephalus zealandicus* Broun.



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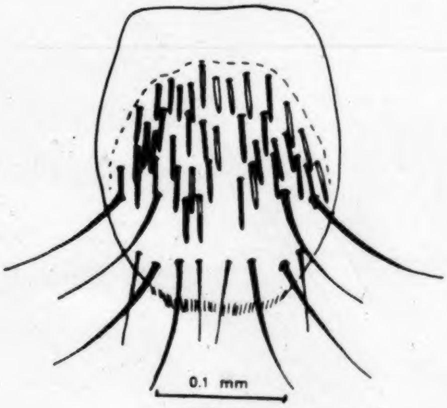

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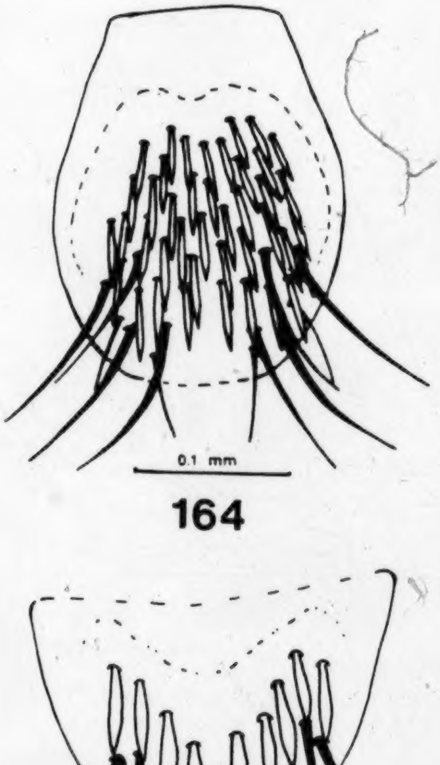

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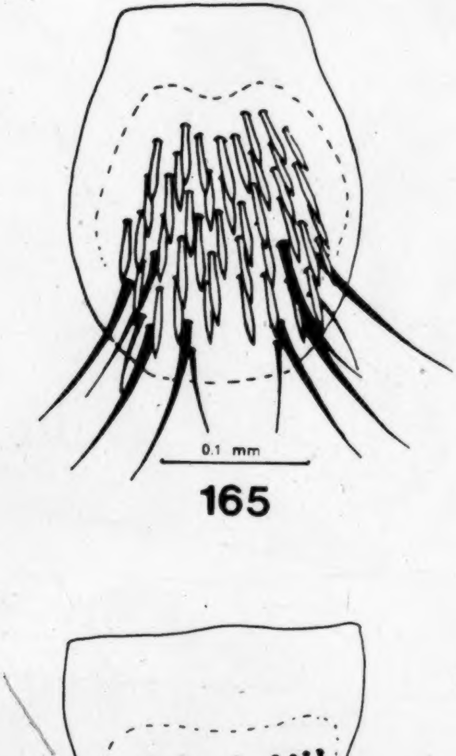

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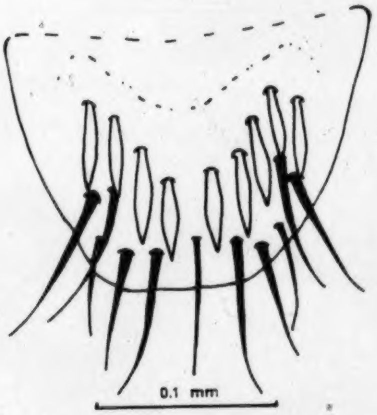

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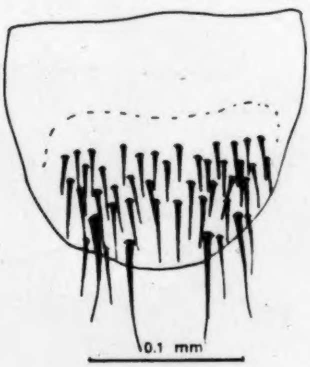

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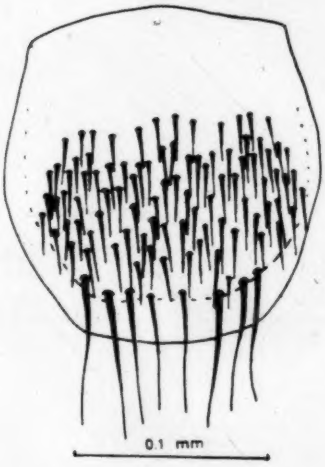

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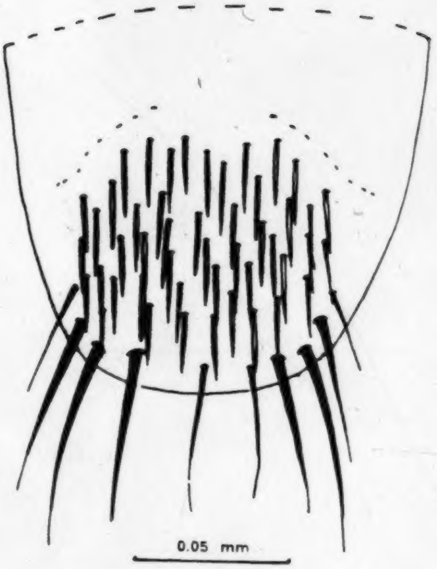

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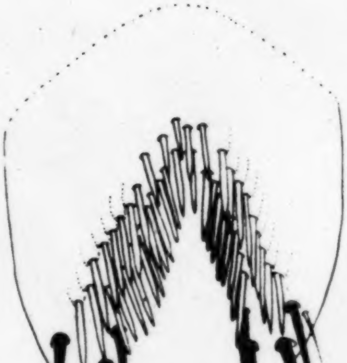

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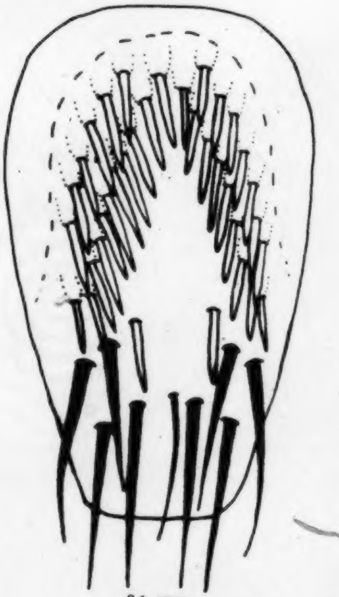

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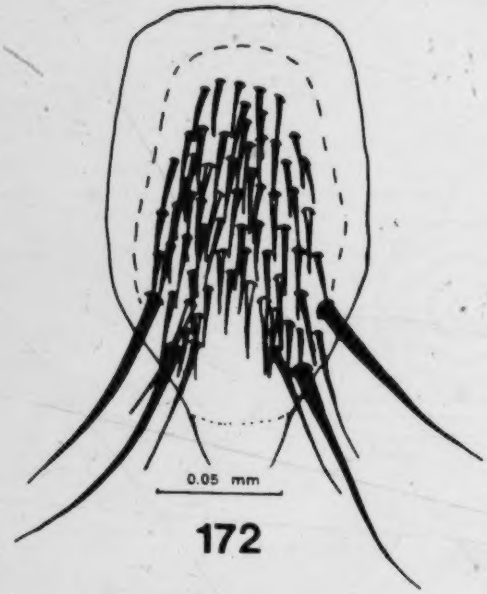
Figures 172-175 Illustrations of tergum 10 of adult Gyrophaenina. Fig. 172. *Pseudoligota varians* Cam. Fig. 173. *Pseudoligota affinis* Cam. Fig. 174. *Brachycara* sp. (prob. *B. crassa* Sharp). Fig. 175. *Agaricomorpha apachaena* (Seev.).



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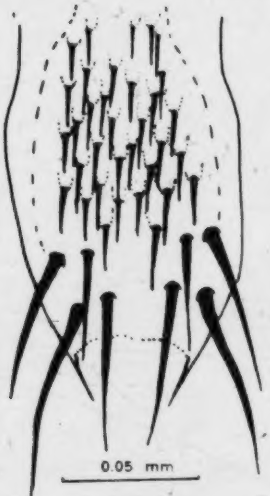

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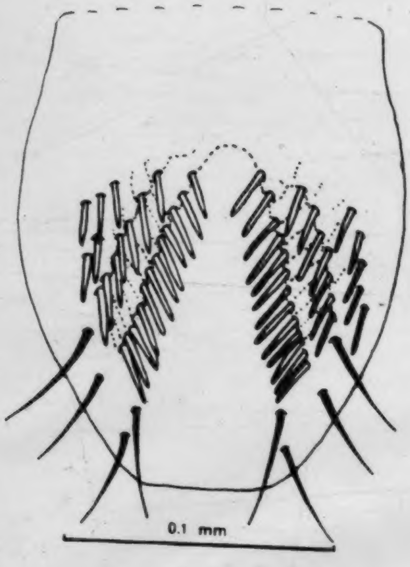

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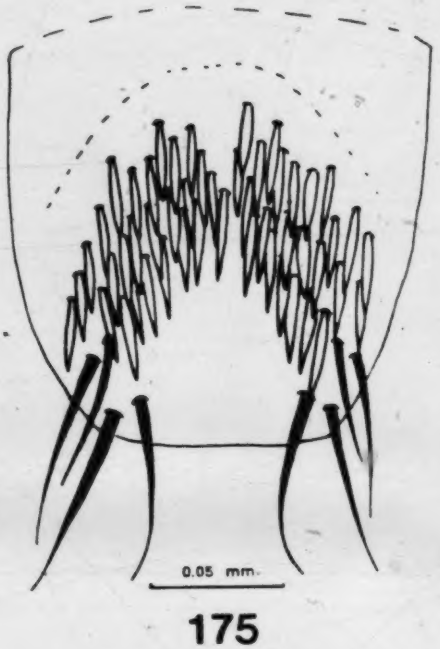

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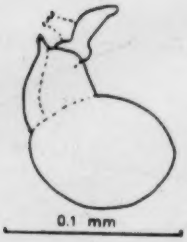
Figures 176-183. Illustrations of spermathecae of adult female Gyrophaenina. Fig. 176. *Gyrophaena nana* Payk. Fig. 177. *Gyrophaena blackwelderi* Seev. Fig. 178. *Gyrophaena frosti* Seev. Fig. 179. *Phanerota fasciata* (Say). Fig. 180. *Phanerota (Acanthophaena) insigniventris* (Cam.) Fig. 181. *Eumicrota corruscula* (Erichson). Fig. 182. *Encephalus complicans* Kirby. Fig. 183. *Encephalus zealandicus* Broun.



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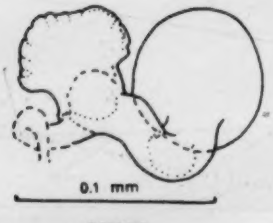

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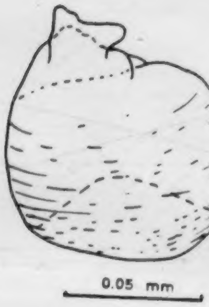

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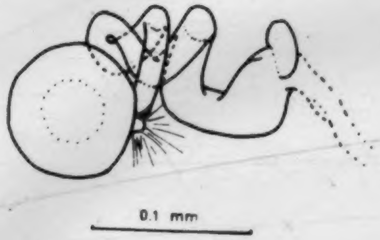

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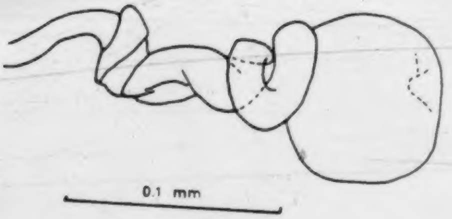

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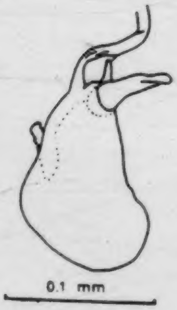

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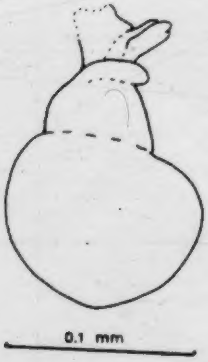

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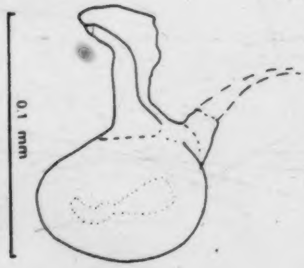

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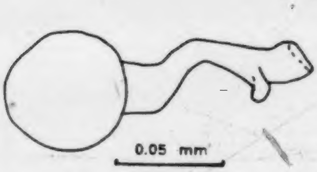
Figures 184-190. Illustrations of spermathecae of adult female Gyrophaenina. Fig. 184. *Probrachida* undescr. sp. Fig. 185. *Brachida exigua* Heer. Fig. 186. *Agaricochara laevicollis* Kr. Fig. 187. *Sternotropa brevicornis* Cam. Fig. 188. *Pseudoligota varians* Cam. Fig. 189. *Brachycara* sp. (prob. *B. crassa* Sharp). Fig. 190. *Agaricomorpha apachaena* (Seev.).

Figure 191. *Bolitochara lunulata* Gyll., spermatheca.



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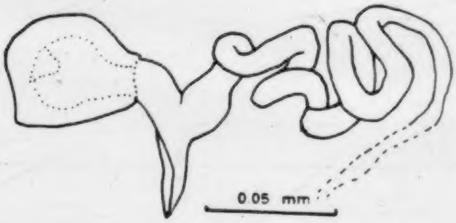

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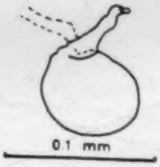

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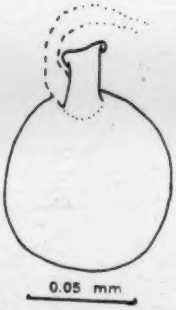

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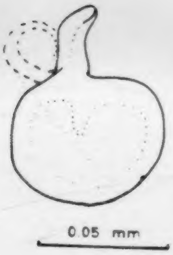

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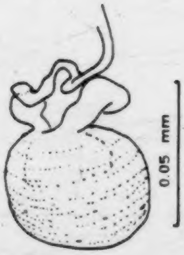

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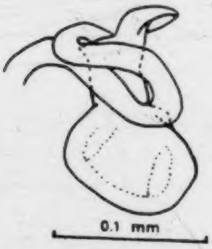

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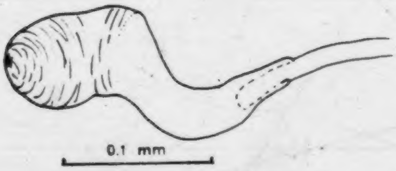

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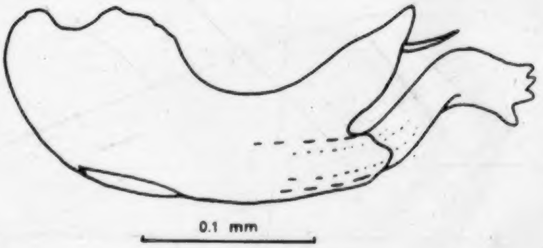

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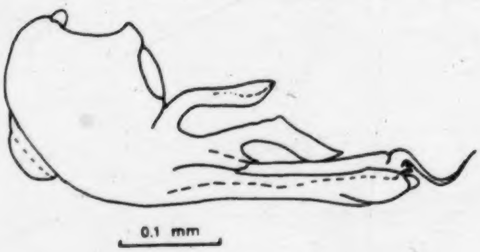

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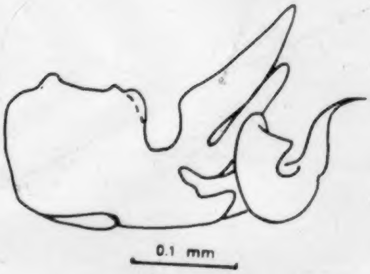

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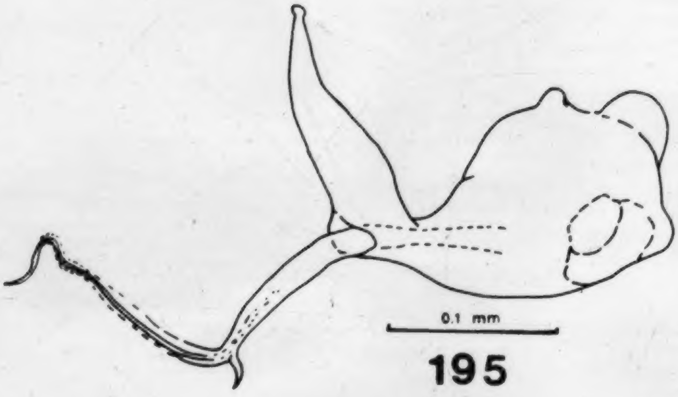

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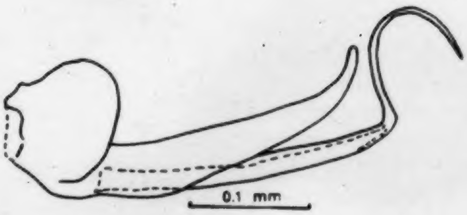

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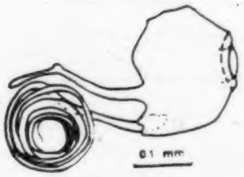

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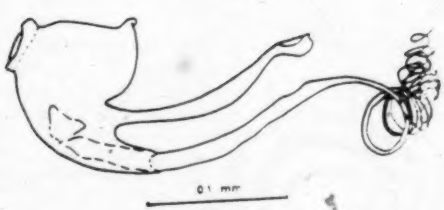

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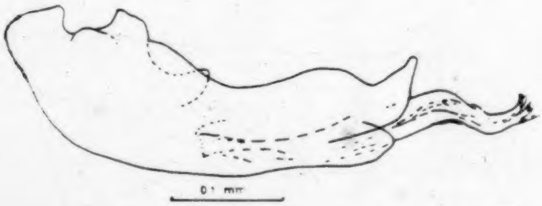

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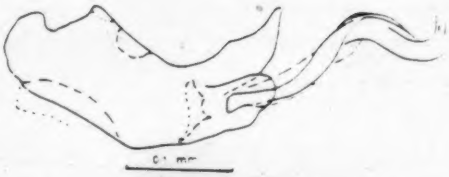

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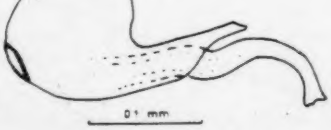

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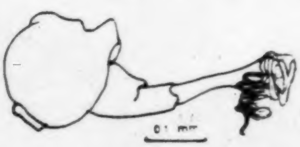

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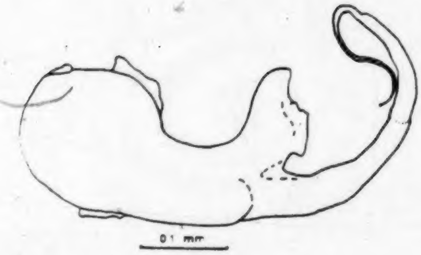

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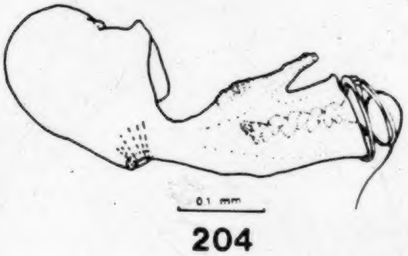

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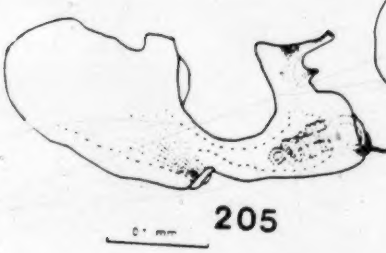

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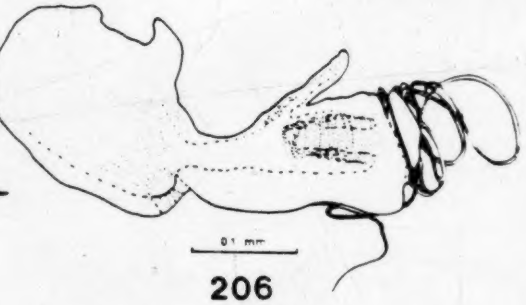

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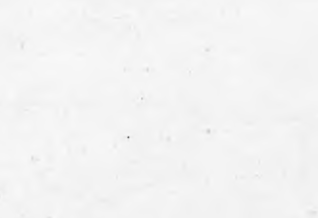

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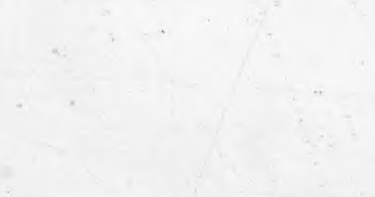

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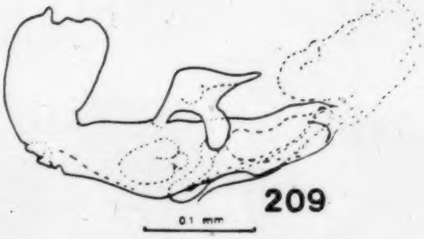

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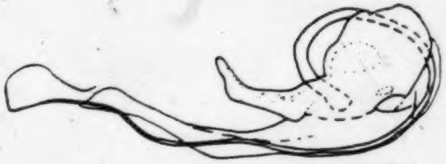

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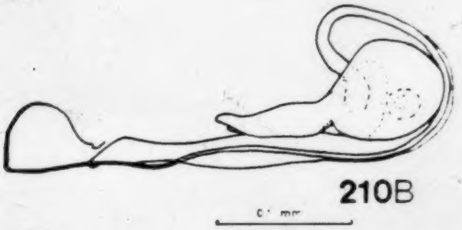

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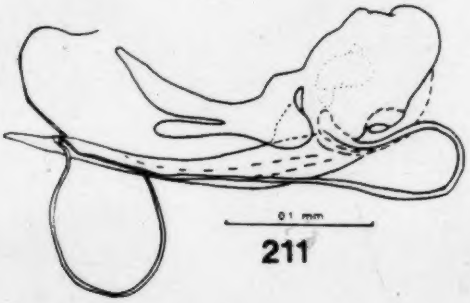

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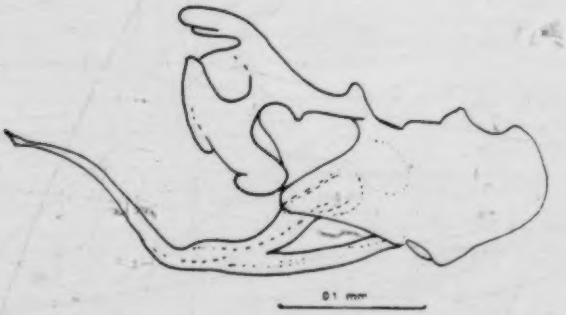

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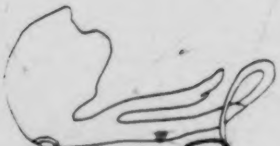

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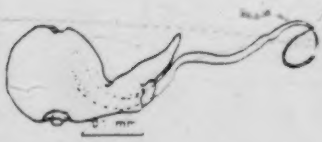

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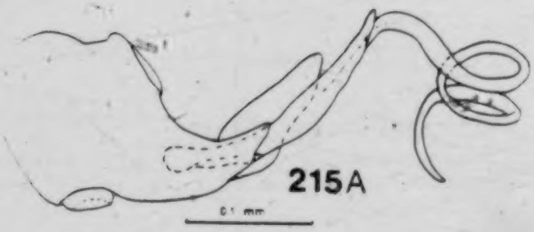

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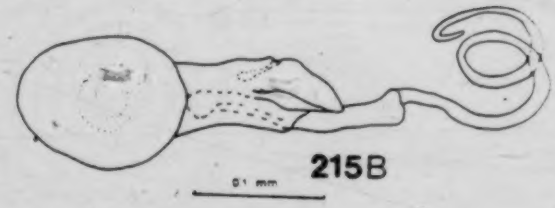

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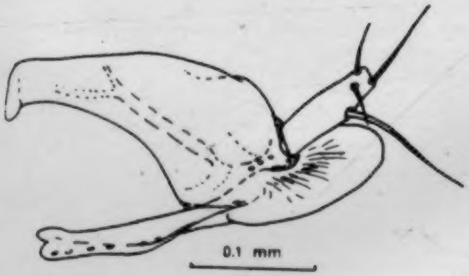

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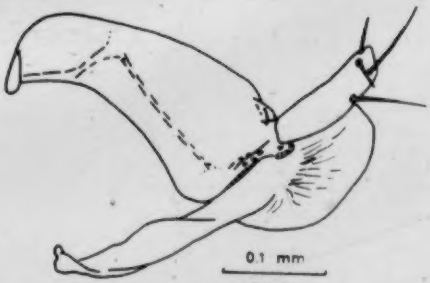

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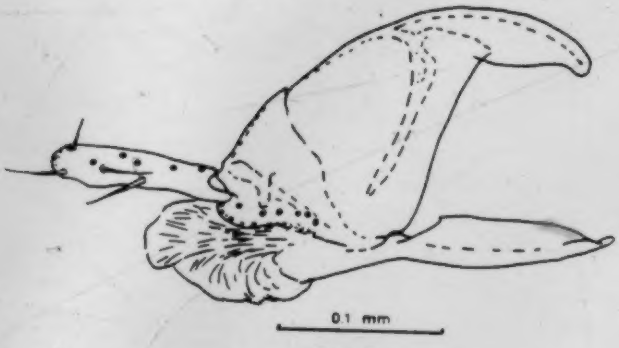

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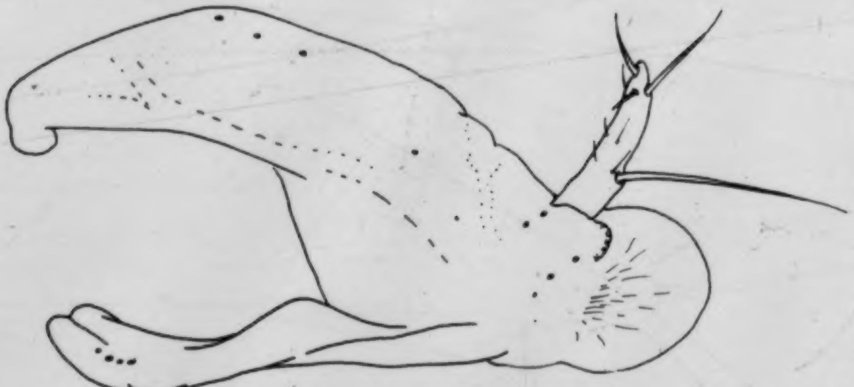

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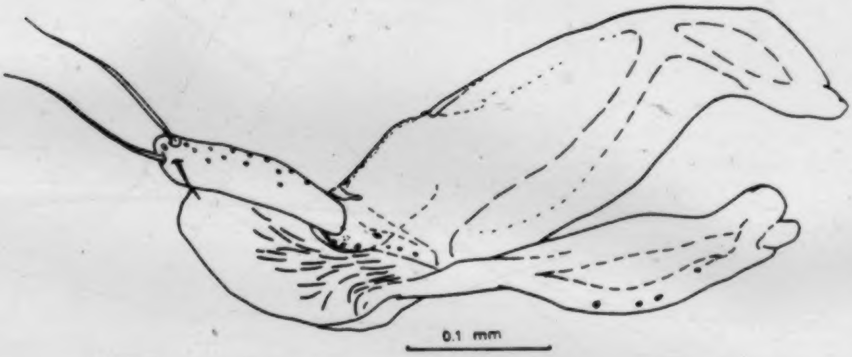

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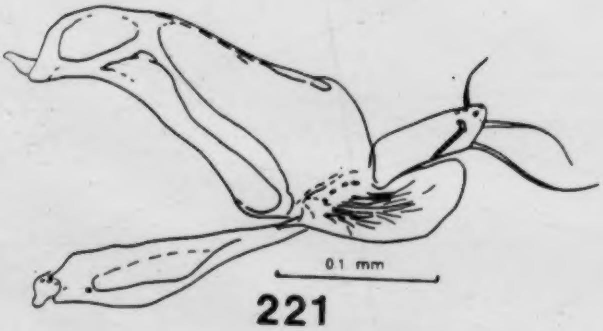

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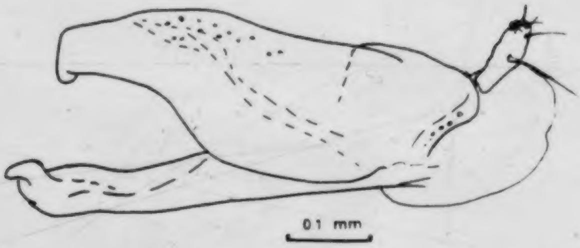

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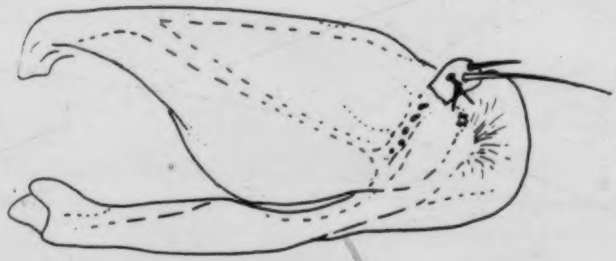

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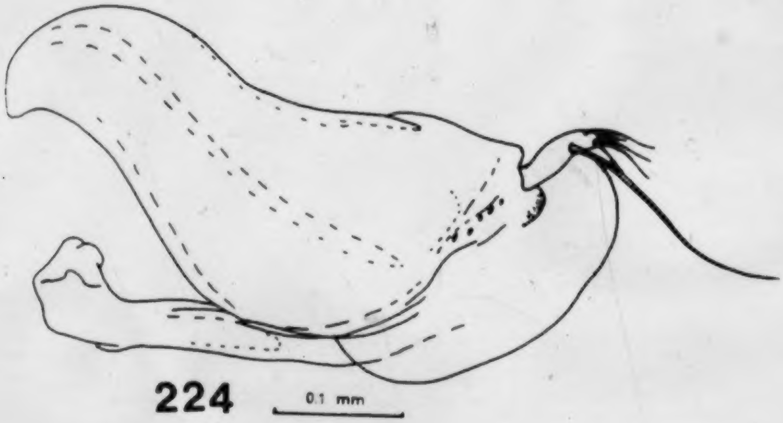

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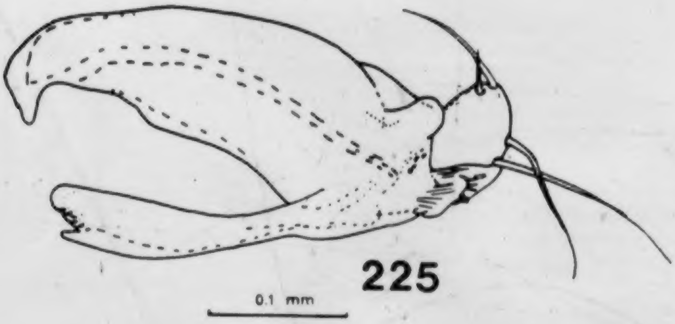

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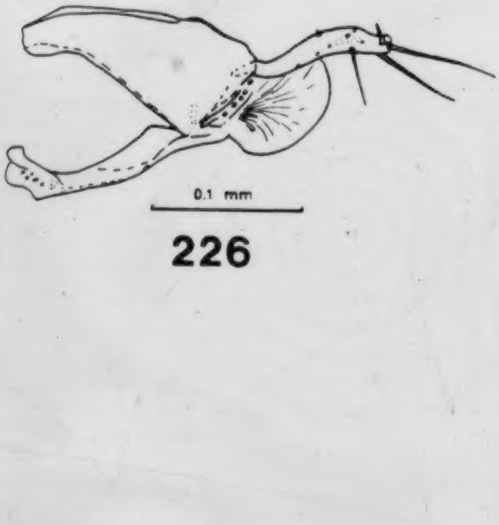

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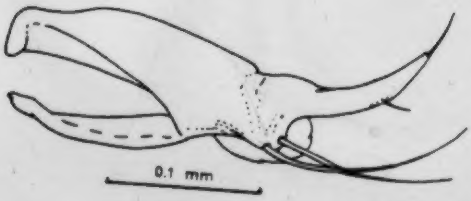

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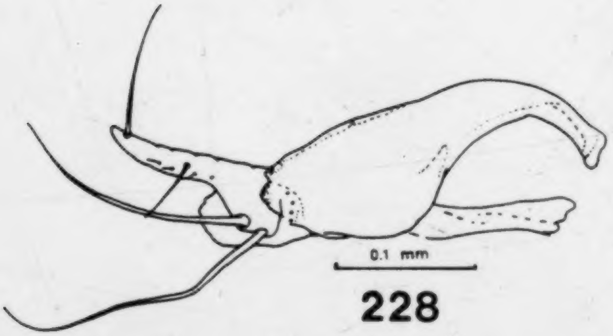

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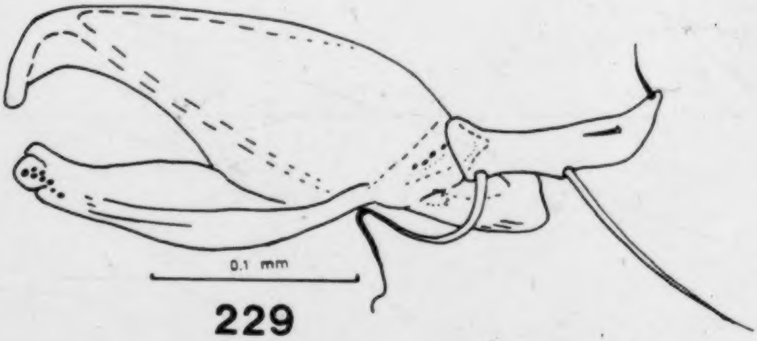

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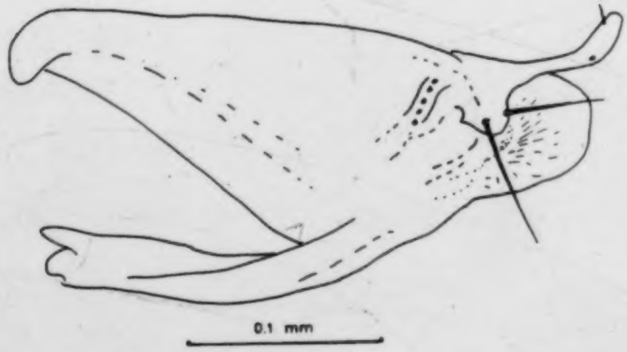

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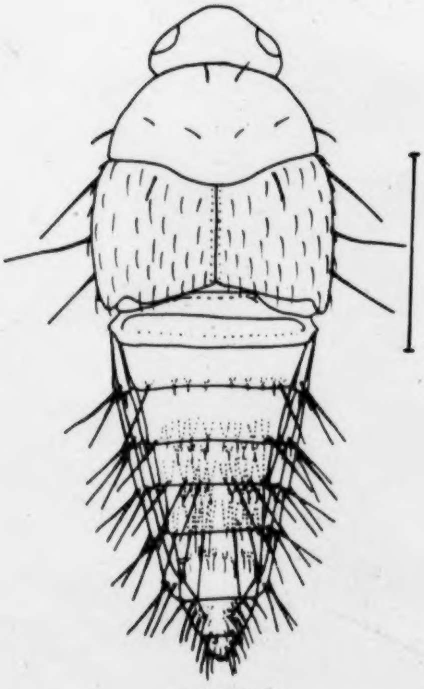
Figure 231. *Adelarthra barbari* Cam., dorsal aspect of body. (Scale line = 0.3mm).

Figure 232. *Brachycara* sp.; larva, instar 3; apical aspect of tergum 8 showing brush-like setae.



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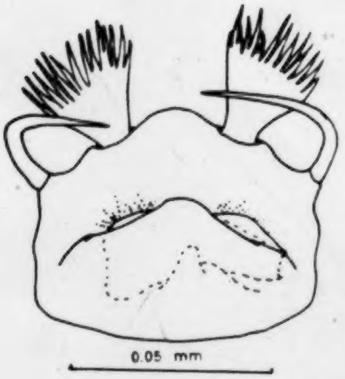

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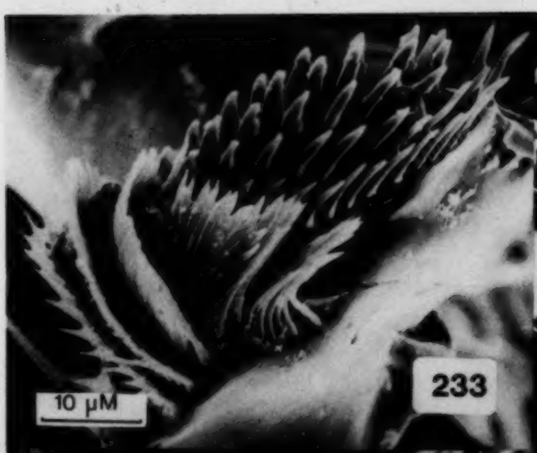
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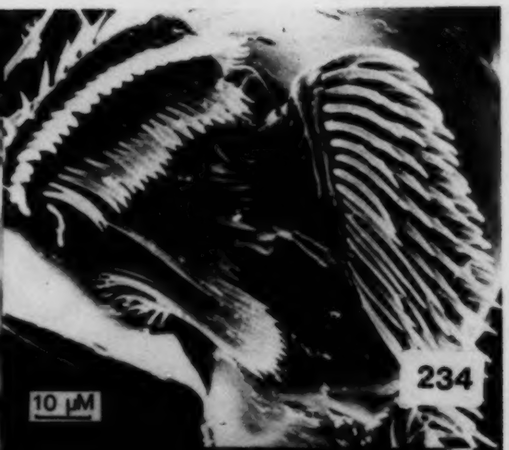
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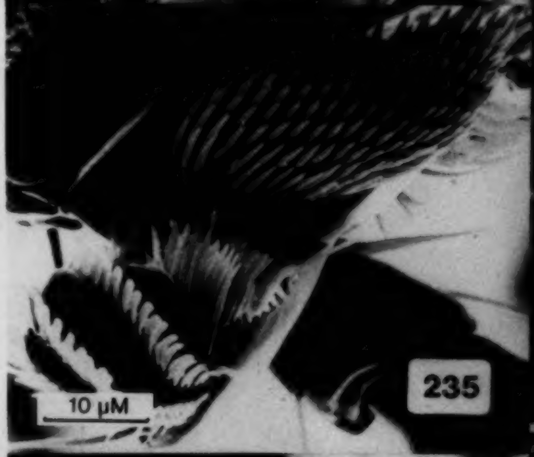
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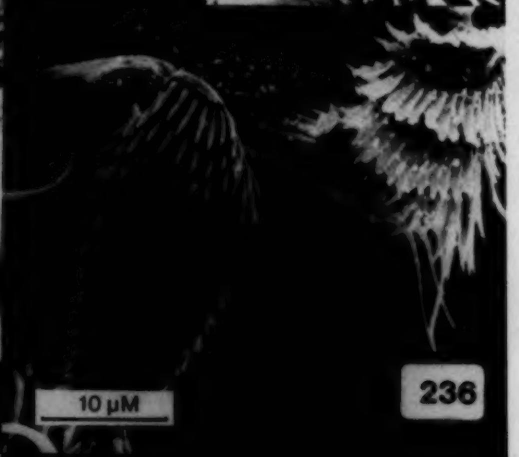
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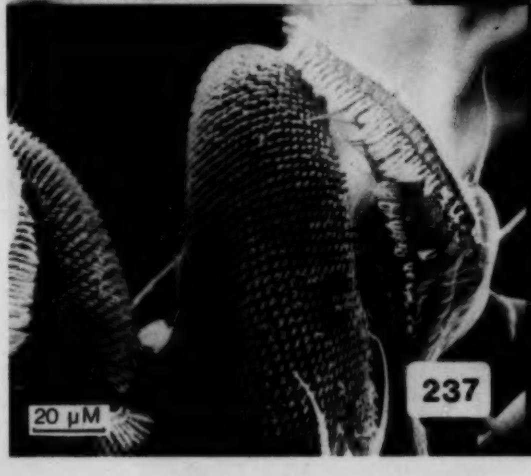
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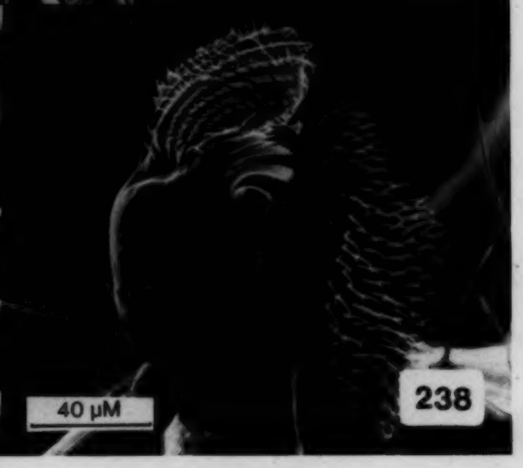
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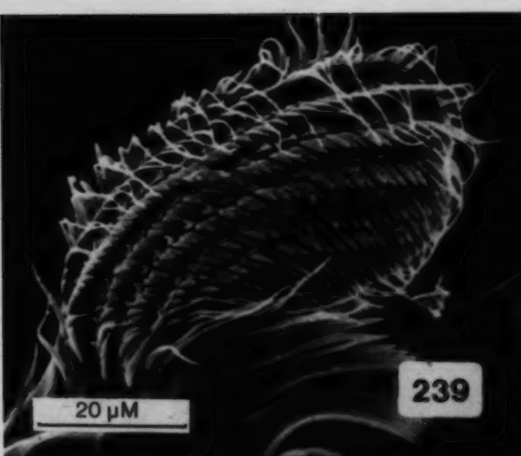

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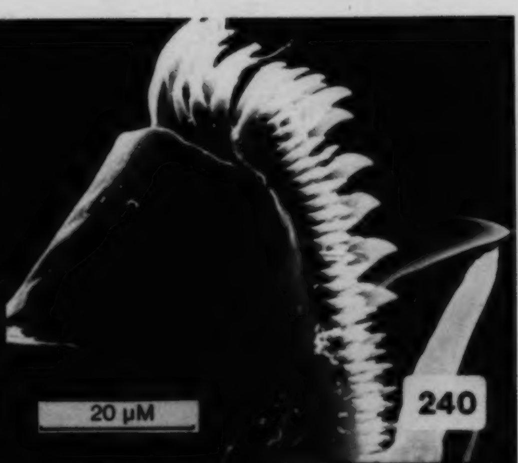

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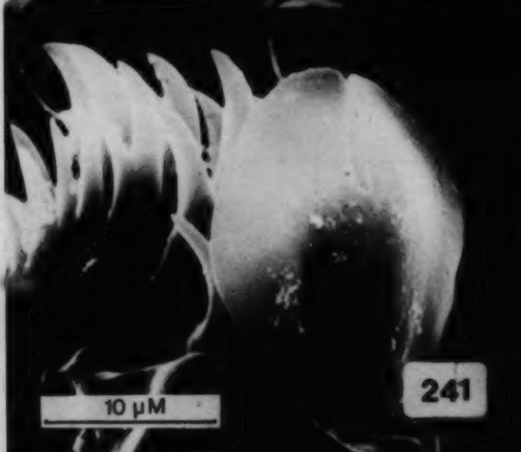

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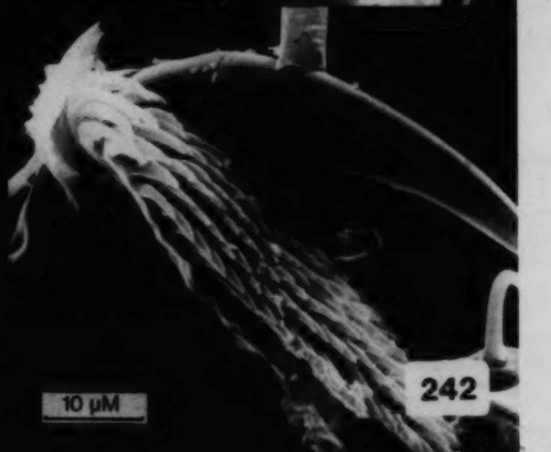
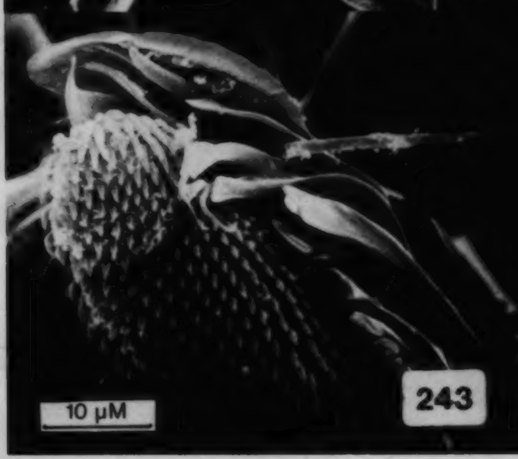
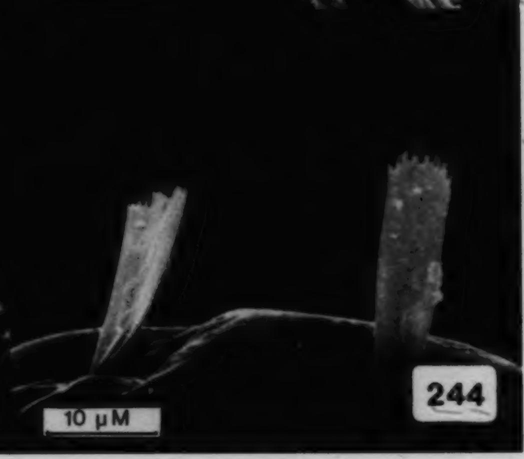


242



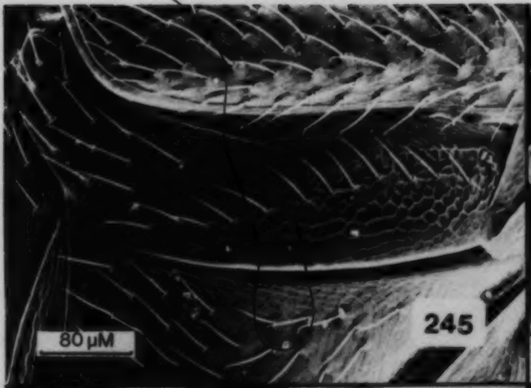
243

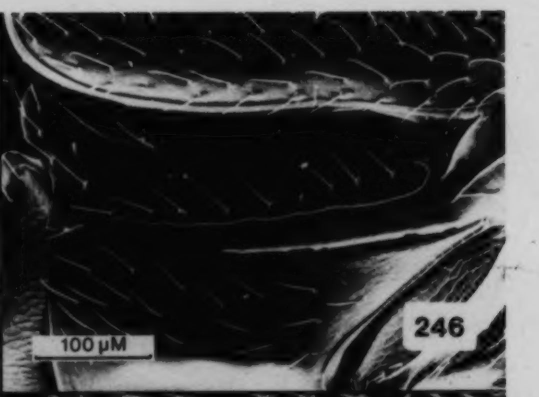


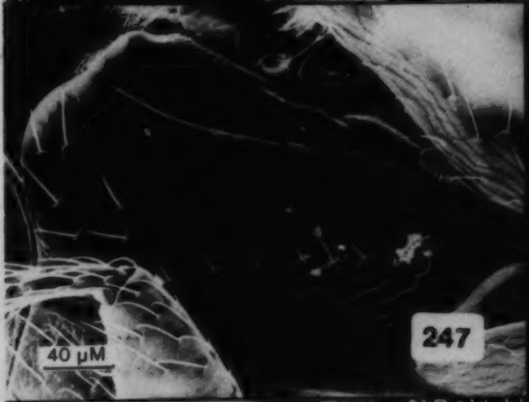
244

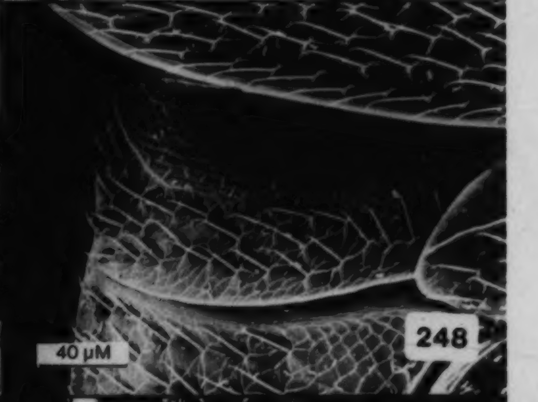
Figures 245-249. SEM micrographs of metepisterna and metepimera of adult Gyrophaenina. Fig. 245. *Gyrophaena nana* Payk. Fig. 246. *Gyrophaena gilvicollis* Csy. Fig. 247. *Eumicrota corruscula* (Erichson). Fig. 248. *Agaricomorpha apachaena* (Seev.). Fig. 249. *Brachycara* sp. (prob. *B. crassa* Sharp).

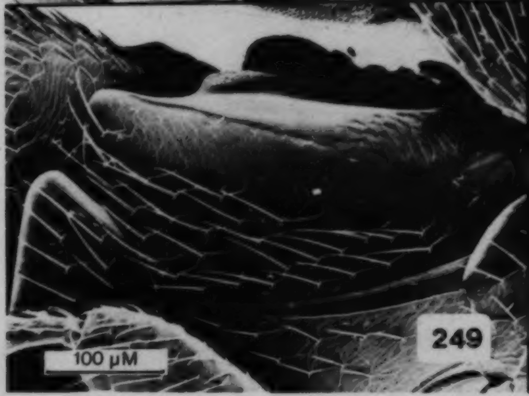
Figure 250. *Brachycara* sp. (prob. *B. crassa* Sharp), adult, ventral aspect, mesosternum and metasternum.


80 µM
245


100 µM
246


40 µM
247


40 µM
248


100 µM
249

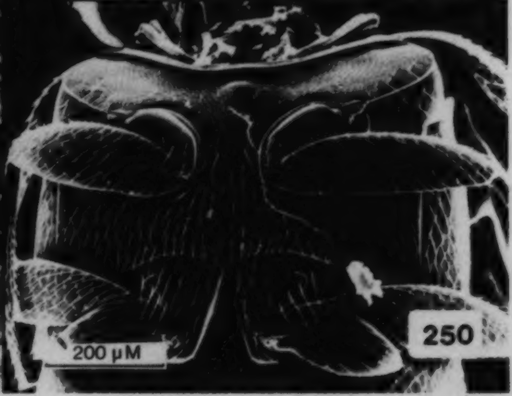
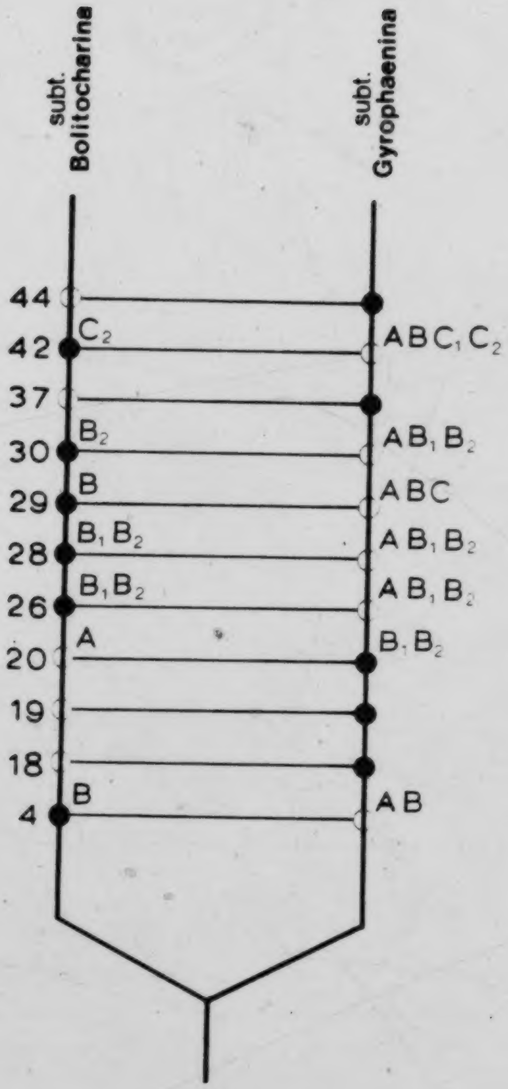
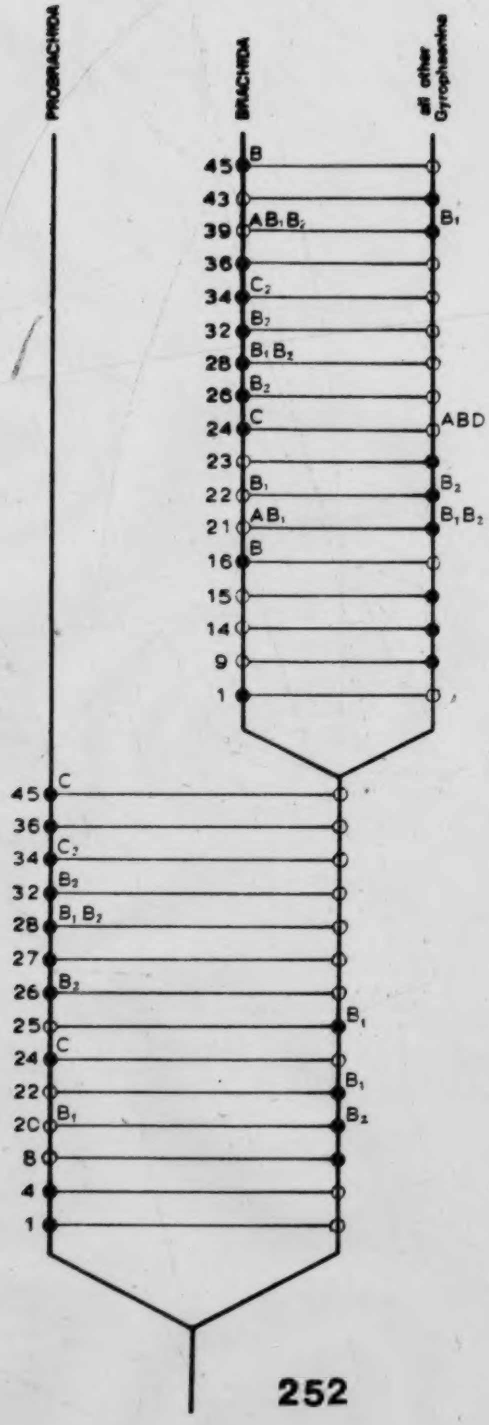

200 µM
250

Figure 251. Hypothesized cladistic relationships between subtribes Bolitocharina and Gyrophaenina.


subt. Bolitocharina
subt. Gyrophaenina
44
42
$C_2$
$ABC_1C_2$
37
30
$B_2$
$AB_1B_2$
29
B
ABC
28
$B_1B_2$
$AB_1B_2$
26
$B_1B_2$
$AB_1B_2$
20
A
$B_1B_2$
19
18
4
B
AB

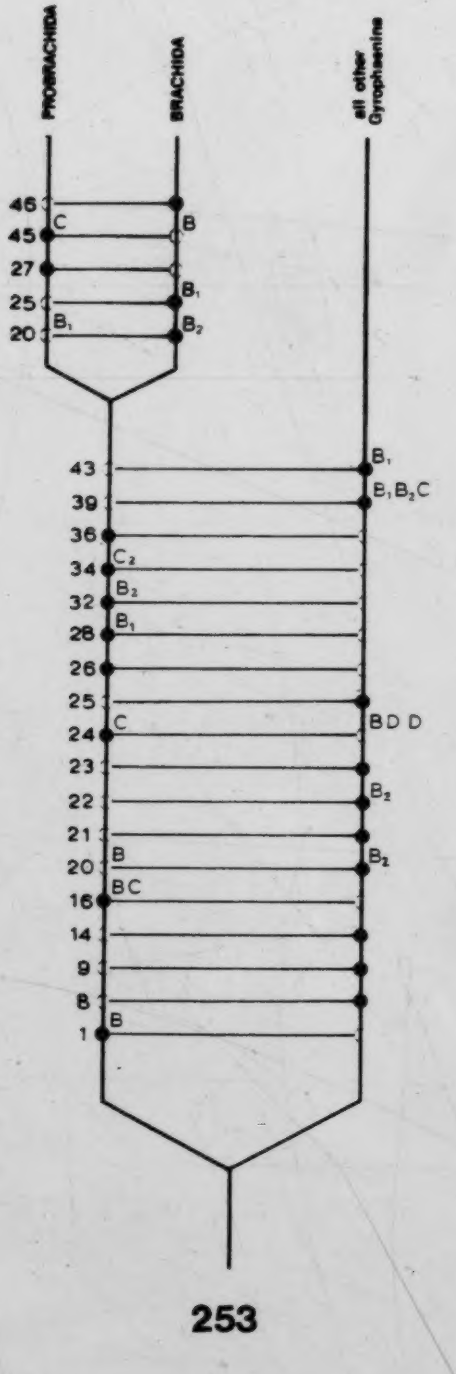
251

Figure 252. Hypothesized cladistic relationships among *Probrachida*, *Brachida* and all other Gyrophaenina, Hypothesis I.


PROBRACHIDA
BRACHIDA
all other Gyrophaenina
45 B
43
39 AB₁B₂ B₁
36
34 C₂
32 B₂
28 B₁B₂
26 B₂
24 C ABD
23
22 B₁ B₂
21 AB₁ B₁B₂
16 B
15
14
9
1
45 C
36
34 C₂
32 B₂
28 B₁B₂
27
26 B₂
25 B₁
24 C
22 B₁
20 B₁ B₂
8
4
1

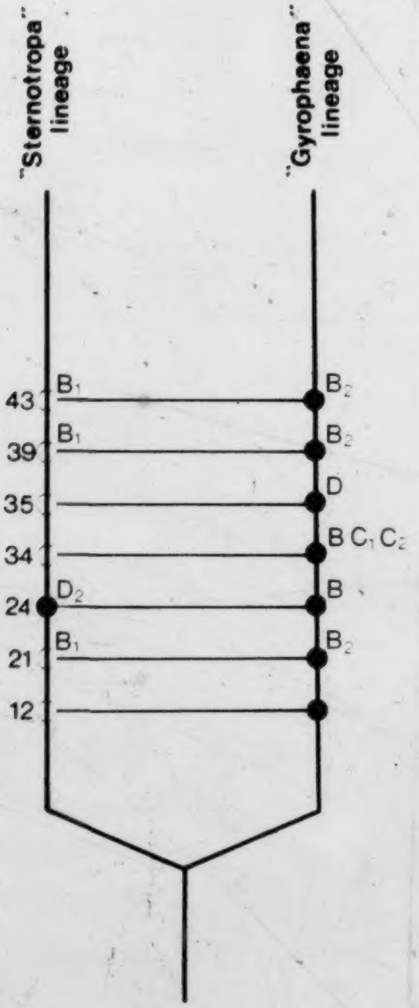
252

Figure 253. Hypothesized cladistic relationships among *Probrachida*, *Brachida* and all other Gyrophaenina, Hypothesis II.


PROBRACHIDA
BRACHIDA
all other Gyrophaenina
46
45
27
25
20
C
B
B₁
B₁
B₂
43
39
36
34
32
28
26
25
24
23
22
21
20
16
14
9
8
1
B₁
B₁B₂C
C₂
B₂
B₁
C
BD D
B₂
B
B₂
BC
B

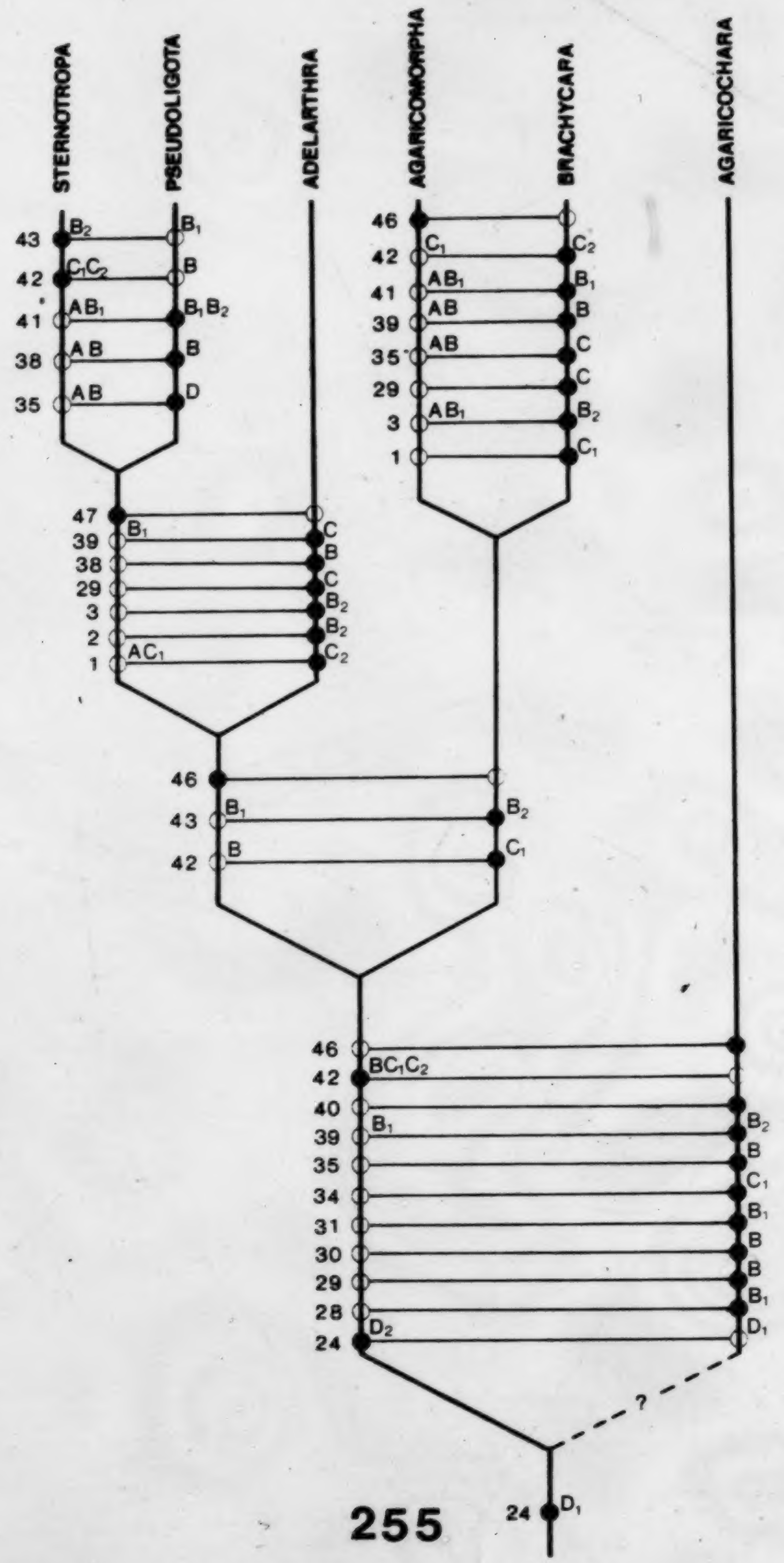
253

Figure 254. Hypothesized cladistic relationships between "Sternotropa" and "Gyrophaena" lineages.


"Sternotropa" lineage
"Gyrophaena" lineage
43
$B_1$
$B_2$
39
$B_1$
$B_2$
35
D
34
B $C_1$ $C_2$
24
$D_2$
B
21
$B_1$
$B_2$
12

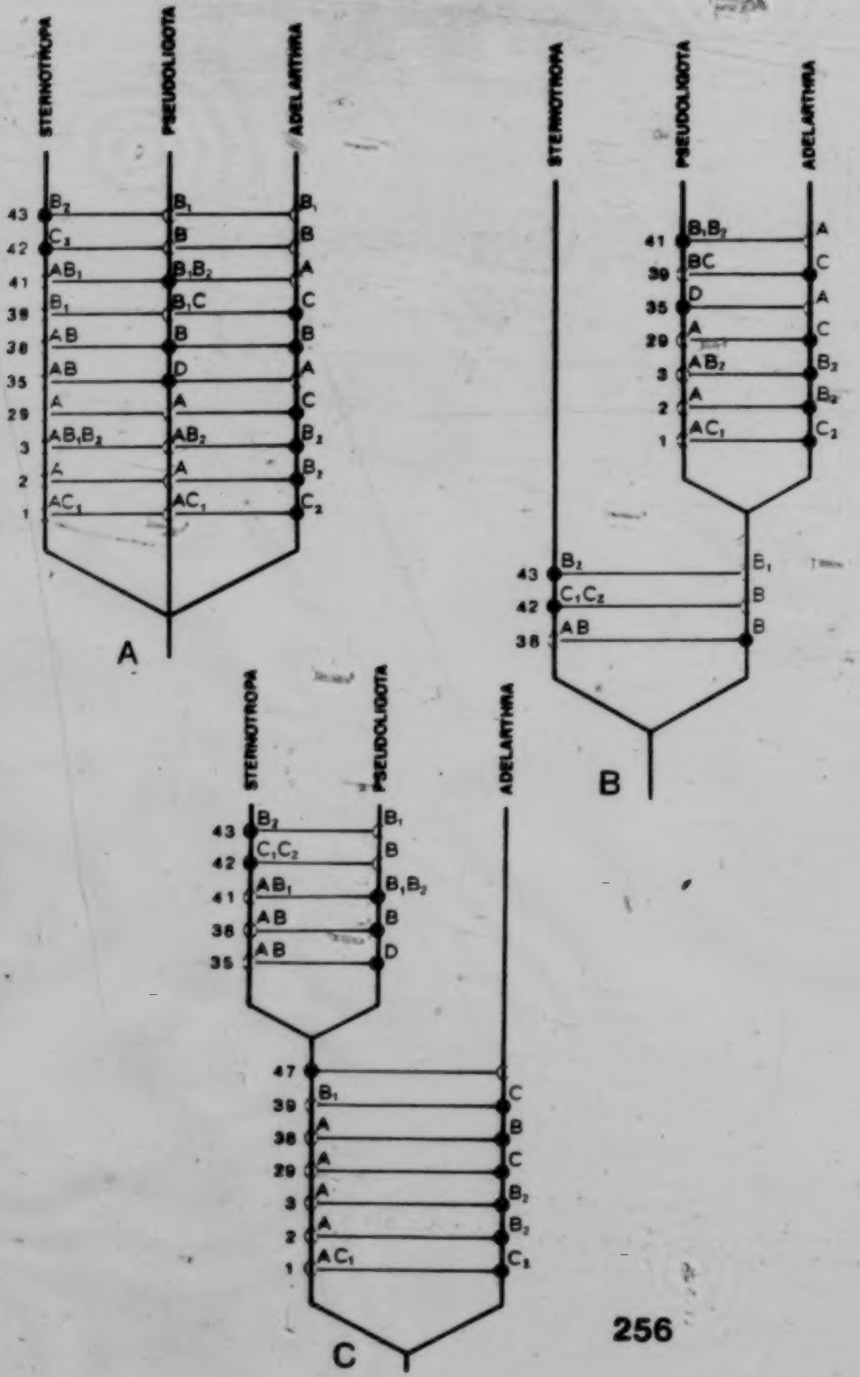
254

Figure 255. Hypothesized cladistic relationships among members of the "Sternotropa" lineage.


STERNOTROPA
PSEUDOLIGOTA
ADELARTHRA
AGARICOMORPHA
BRACHYCARA
AGARICOCHARA
43 B2 B1
42 C1C2 B
41 AB1 B1B2
38 AB B
35 AB D
46
42 C1 C2
41 AB1 B1
39 AB B
35 AB C
29 C
3 AB1 B2
1 C1
47
39 B1 C
38 B
29 C
3 B2
2 B2
1 AC1 C2
46
43 B1 B2
42 B C1
46
42 BC1C2
40 B2
39 B1 B
35 C1
34 B1
31 B
30 B
29 B1
28 D1
24 D2
?
24 D1

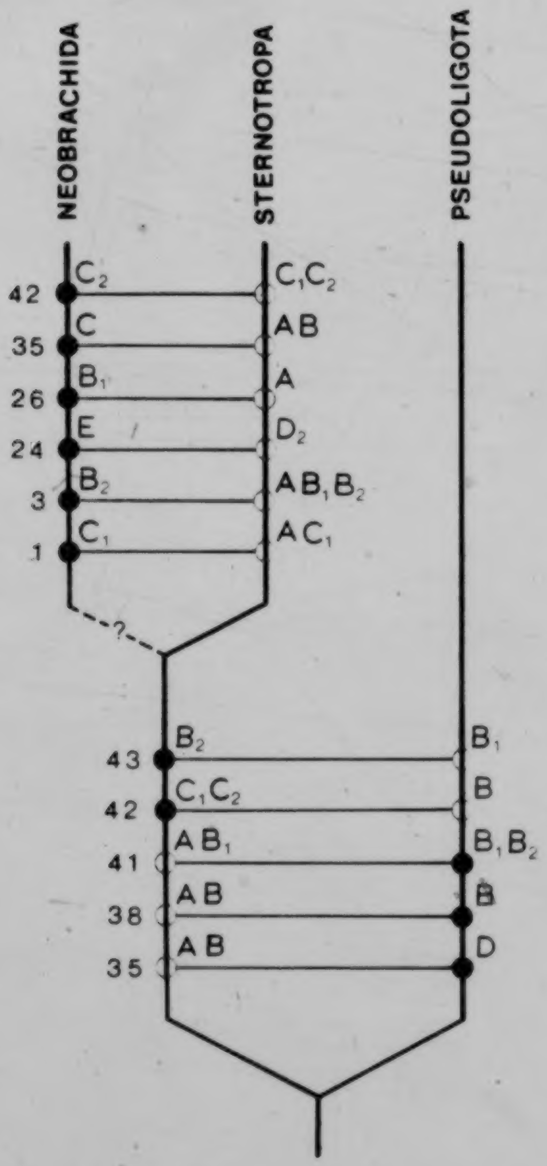
255

Figure 256. Possible cladistic relationships of *Adelarthra* Cam. A) Hypothesis I. B) Hypothesis II. C) Hypothesis III.


STERNOTROPA
PSEUDOLIGOTA
ADELARTHRA
43
42
41
39
38
35
29
3
2
1
B₂
C₂
AB₁
B₁
AB
AB
A
AB₁B₂
A
AC₁
B₁
B
B₁B₂
B₁C
B
D
A
AB₂
A
AC₁
B₁
B
A
C
B
A
C
B₂
B₂
C₂
A
STERNOTROPA
PSEUDOLIGOTA
ADELARTHRA
41
39
35
29
3
2
1
B₁B₂
BC
D
A
AB₂
A
AC₁
A
C
A
C
B₂
B₂
C₂
43
42
38
B₂
C₁C₂
AB
B₁
B
B
B
STERNOTROPA
PSEUDOLIGOTA
ADELARTHRA
43
42
41
38
35
B₂
C₁C₂
AB₁
AB
AB
B₁
B
B₁B₂
B
D
47
39
38
29
3
2
1
B₁
A
A
A
A
AC₁
C
C
B
C
B₂
B₂
C₁
C

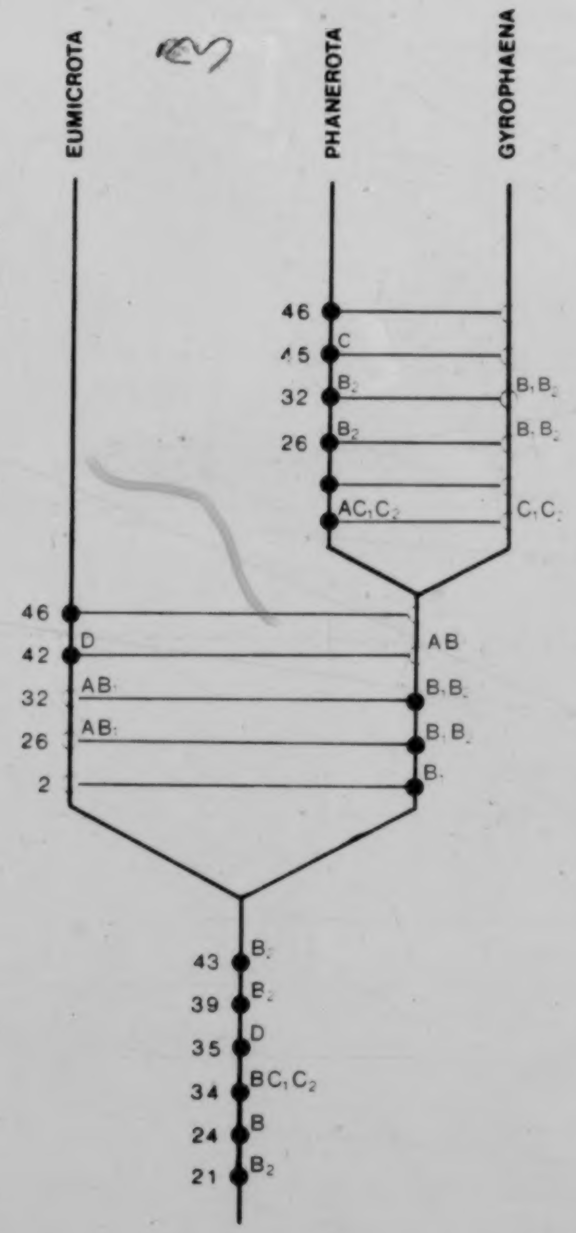
256

Figure 257. Possible cladistic relationships of *Neobrachida* Cam.


NEOBRACHIDA
STERNOTROPA
PSEUDOLIGOTA
42
35
26
24
3
1
$C_2$
C
$B_1$
E
$B_2$
$C_1$
$C_1C_2$
AB
A
$D_2$
$AB_1B_2$
$AC_1$
?
43
42
41
38
35
$B_2$
$C_1C_2$
$AB_1$
AB
AB
$B_1$
B
$B_1B_2$
B
D

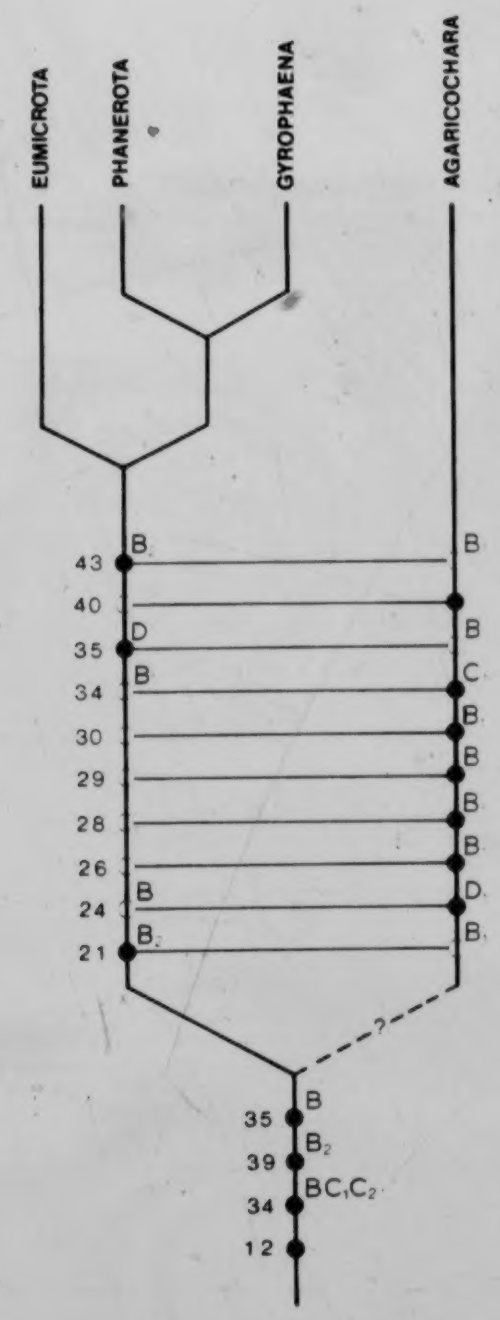
257

Figure 258. Hypothesized cladistic relationships among members of the "Gyrophaena" lineage.


EUMICROTA
PHANEROTA
GYROPHAENA
46
C
45
$B_2$
32
$B_1B_2$
$B_2$
26
$B_1B_2$
$AC_1C_2$
$C_1C_2$
46
AB
D
42
AB
32
$B_1B_2$
AB
26
$B_1B_2$
B
2
$B_2$
43
$B_2$
39
D
35
$BC_1C_2$
34
B
24
$B_2$
21

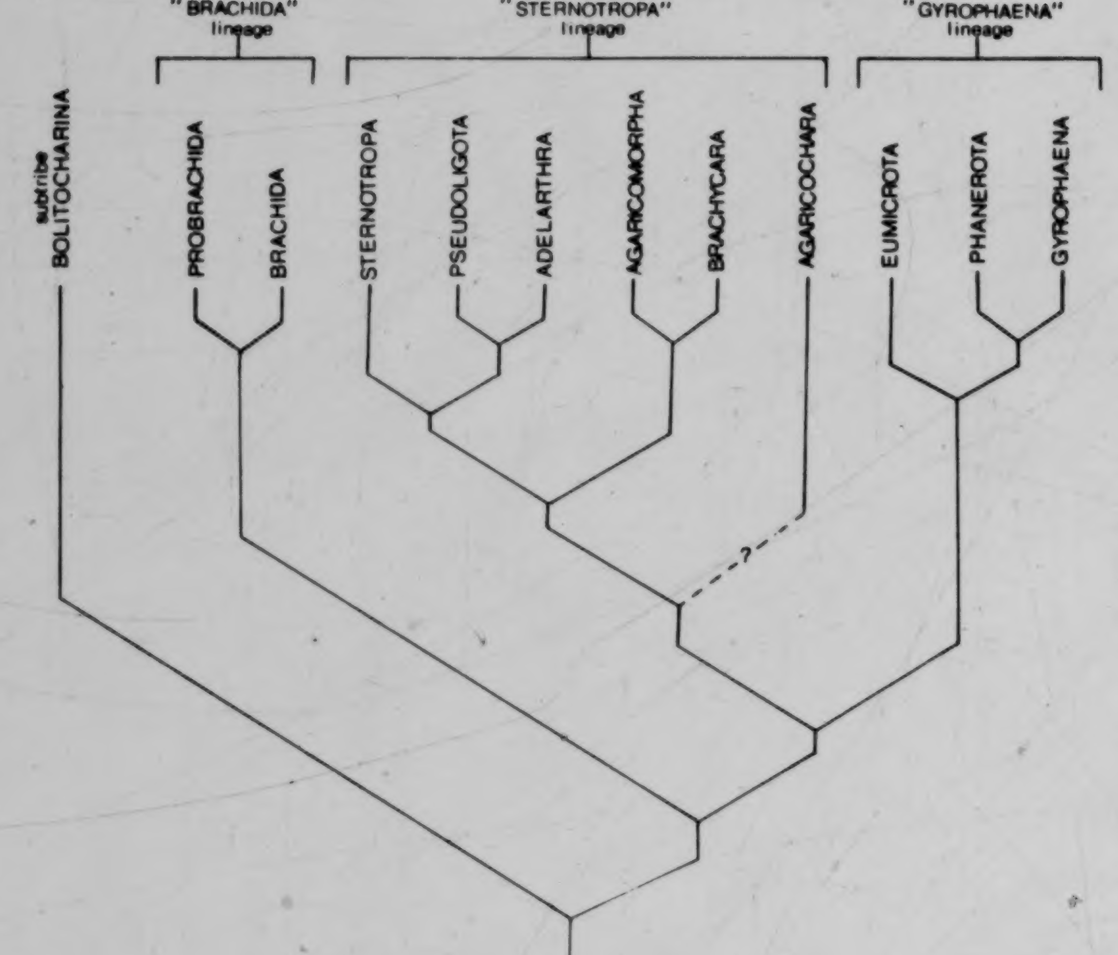
**258**

Figure 259. Hypothesized cladistic relationships of *Agaricochara* Kr., if hypothesized to be a member of the "Gyrophaena" lineage.


EUMICROTA
PHANEROTA
GYROPHAENA
AGARICOCHARA
43 B
40
35 D
34 B
30
29
28
26
24 B
21 B
B
B
C
B
B
B
B
D
B
?
35 B
39 $B_2$
34 $BC_1C_2$
12

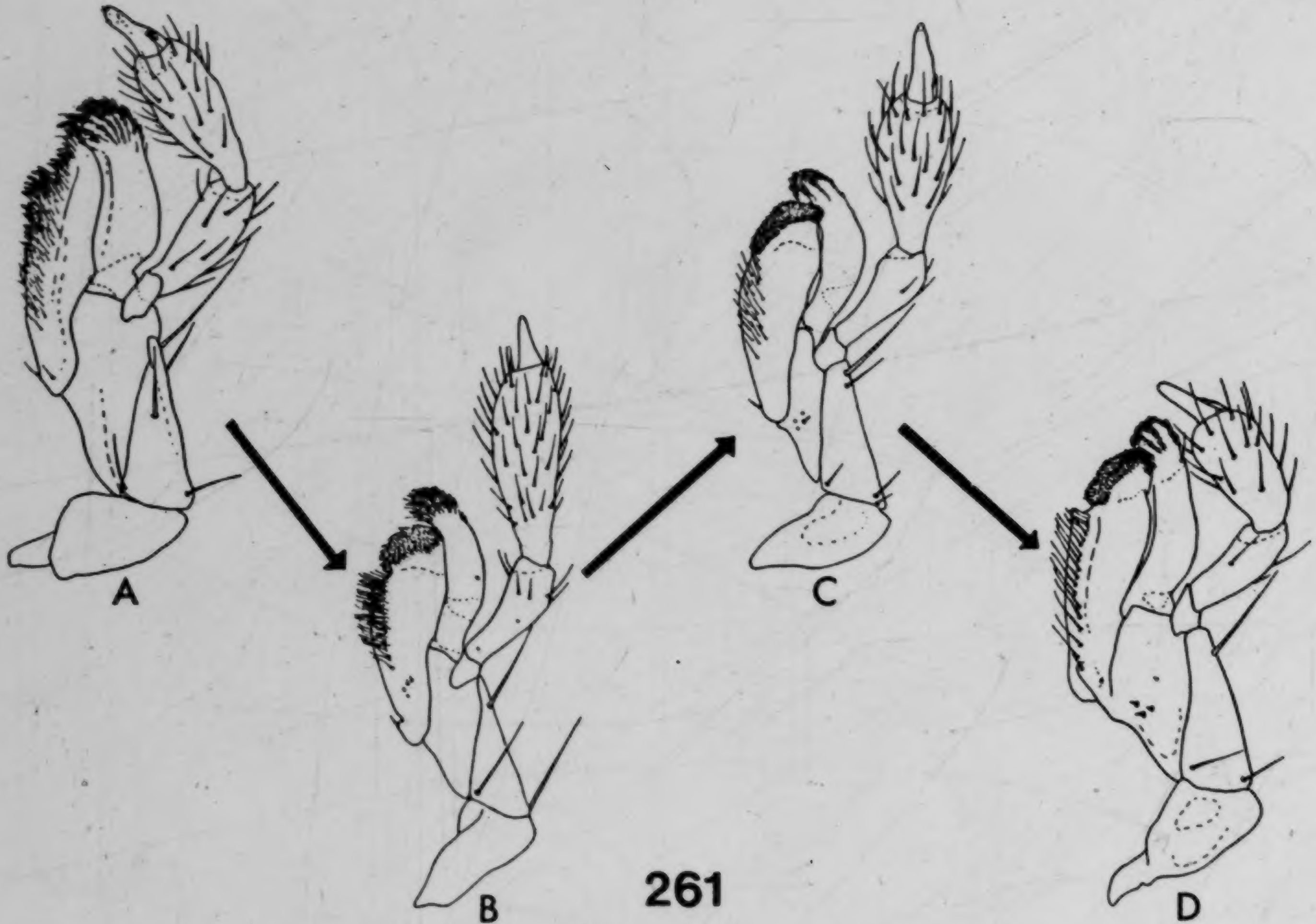
259

Figure 260. Summary of hypothesized cladistic relationships among genera of the Gyrophaenina. (*Neobrachida* and *Encephalus* not included.)


"BRACHIDA" lineage
"STERNOTROPA" lineage
"GYROPHAENA" lineage
subtribe BOLITOCHARINA
PROBRACHIDA
BRACHIDA
STERNOTROPA
PSEUDOLIGOTA
ADELARTHRA
AGARICOMORPHA
BRACHYCARA
AGARICOCHARA
EUMICROTA
PHANEROTA
GYROPHAENA
?

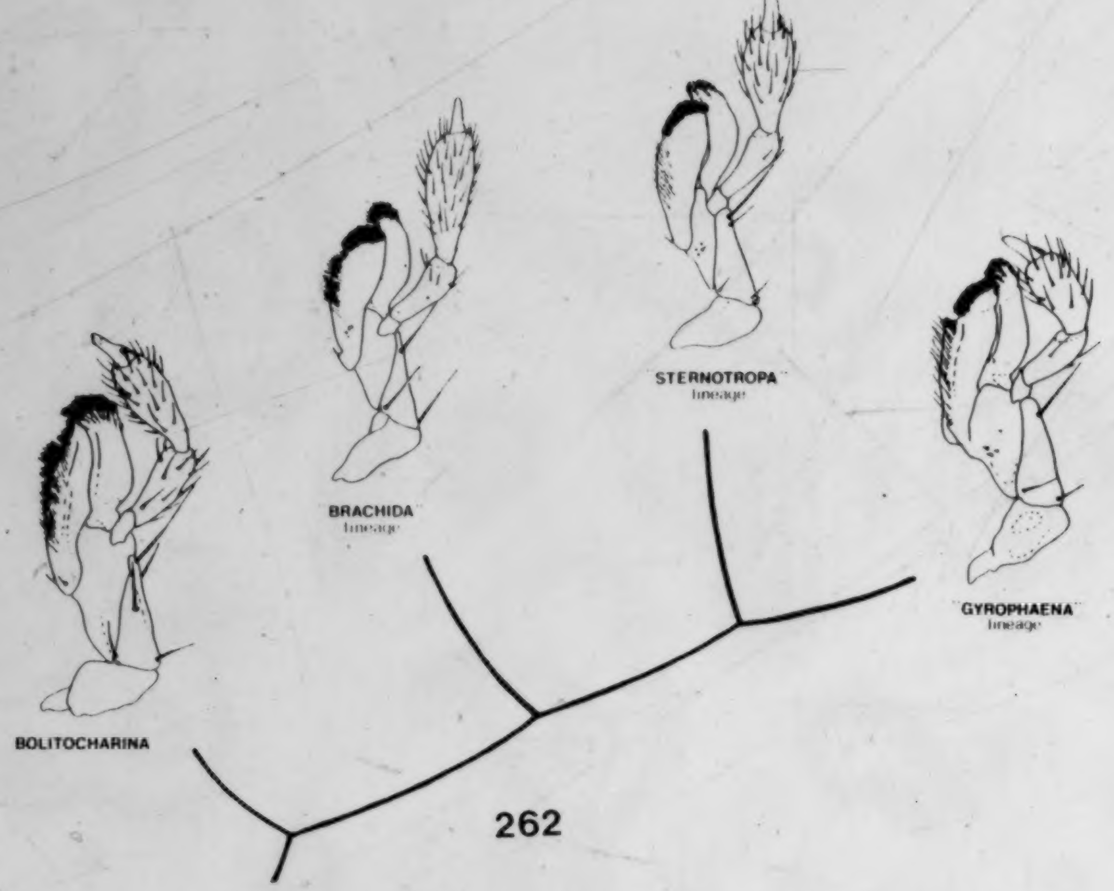
260

Figure 261. Transformation series in maxillary structure among members of subtribe Bolitocharina and Gyrophaenina.



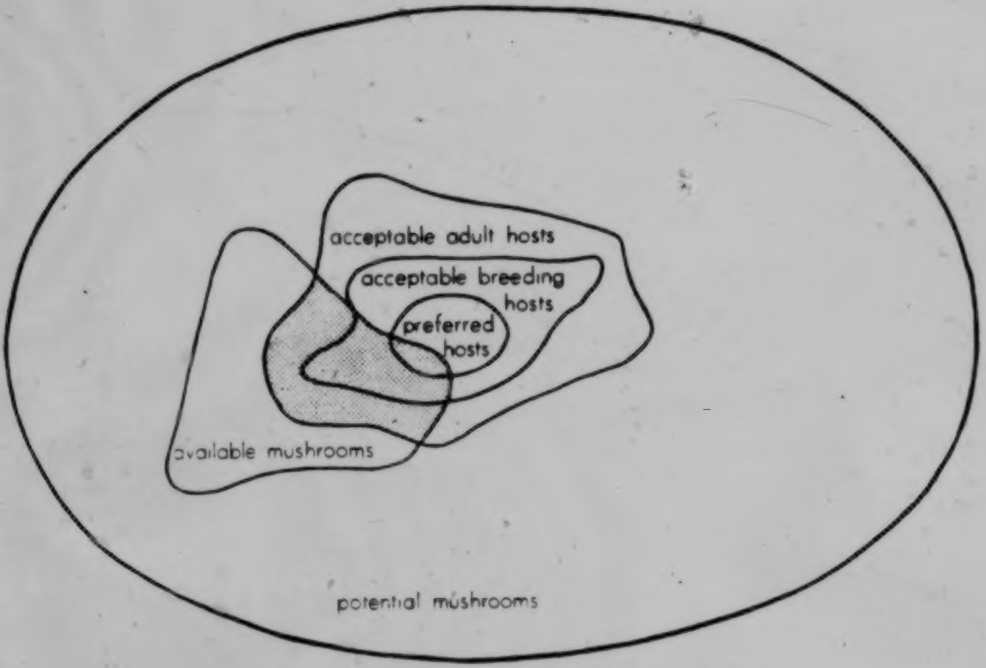
261

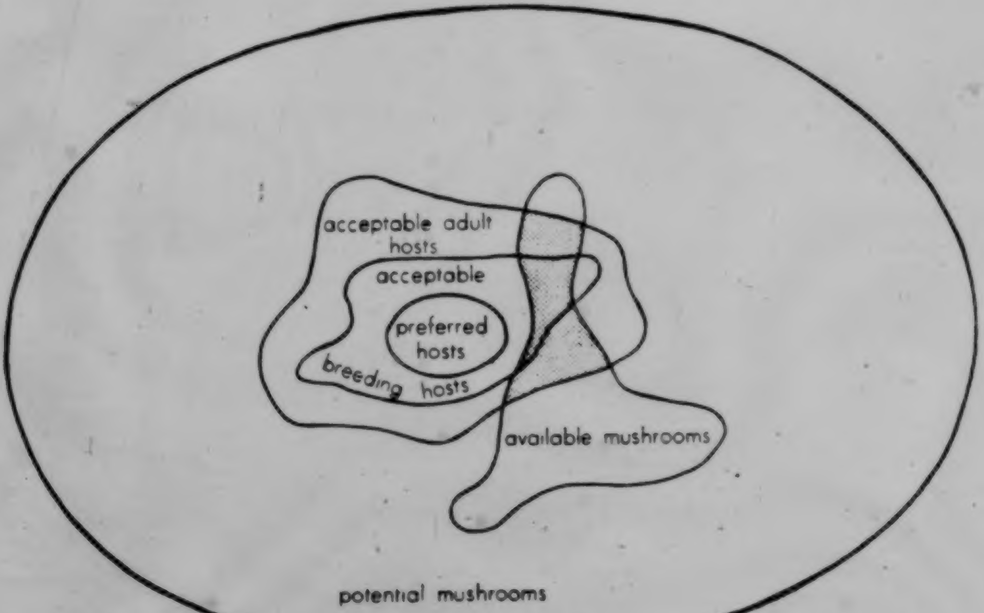
Figure 262. Maxillary forms among members of subtribes Bolitocharina and Gyrophaenina superimposed on a simplified cladogram.


BOLITOCHARINA
"BRACHIDA" lineage
"STERNOTROPA" lineage
"GYROPHAENA" lineage

262

Figure 263. Schematic diagram illustrating how differences in available mushroom flora might overlap different parts of the "acceptability spectrum" of members of a gyrophaenine species.


acceptable adult hosts
acceptable breeding hosts
preferred hosts
available mushrooms
potential mushrooms


acceptable adult hosts
acceptable
preferred hosts
breeding hosts
available mushrooms
potential mushrooms

# Vita

I was born February 23,1947 in Charlotte North Carolina. As the only child of a Baptist Minister, I lived in a number of small towns and communities through out North Carolina during my childhood and teenage years. During this time I exhibited an early interest in natural history and spent much of my childhood in natural history persuits.

In 1965, I entered the University of North Carolina at Charlotte and graduated in 1969 with a B.Sc. in Biology. In September, 1969, I began a M.Sc. program at Appalachian State University at Boone, North Carolina. This was interrupted when I was drafted into the United States Army in June, 1970. I returned from military service and completed an M.A. degree at Appalachian State University in 1972. It was at this time and into the following year that I became interested in beetles in general and fungus staphylinids in particular.

In 1973, I entered Texas A & M University at College Station, Texas, as a Ph.D student, to study ecology of the boll weevil in the cotton ecosystem. It soon became apparent that I was not philosophically suited for a career in economic entomology, so when my supervisor, Dr. Dale Bottrell, resigned his position in 1975, I decided to persue my intense interest in evolution and systematics of insects. I immigrated to Canada and began a Ph.D. program in entomology at the University of Alberta, the results of which are shown in this thesis.